

OSNOVE MIKROBIOLOGIJE

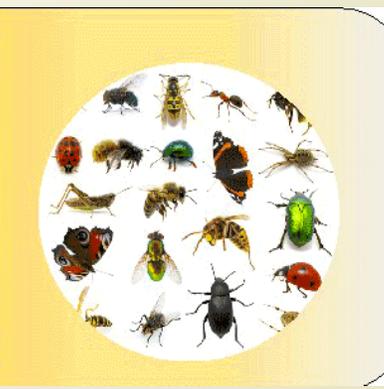
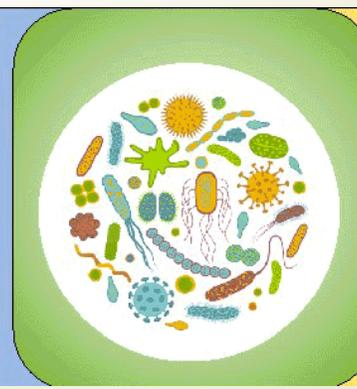
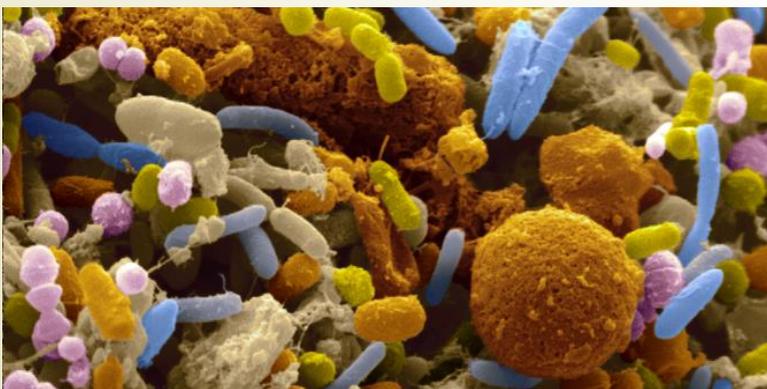
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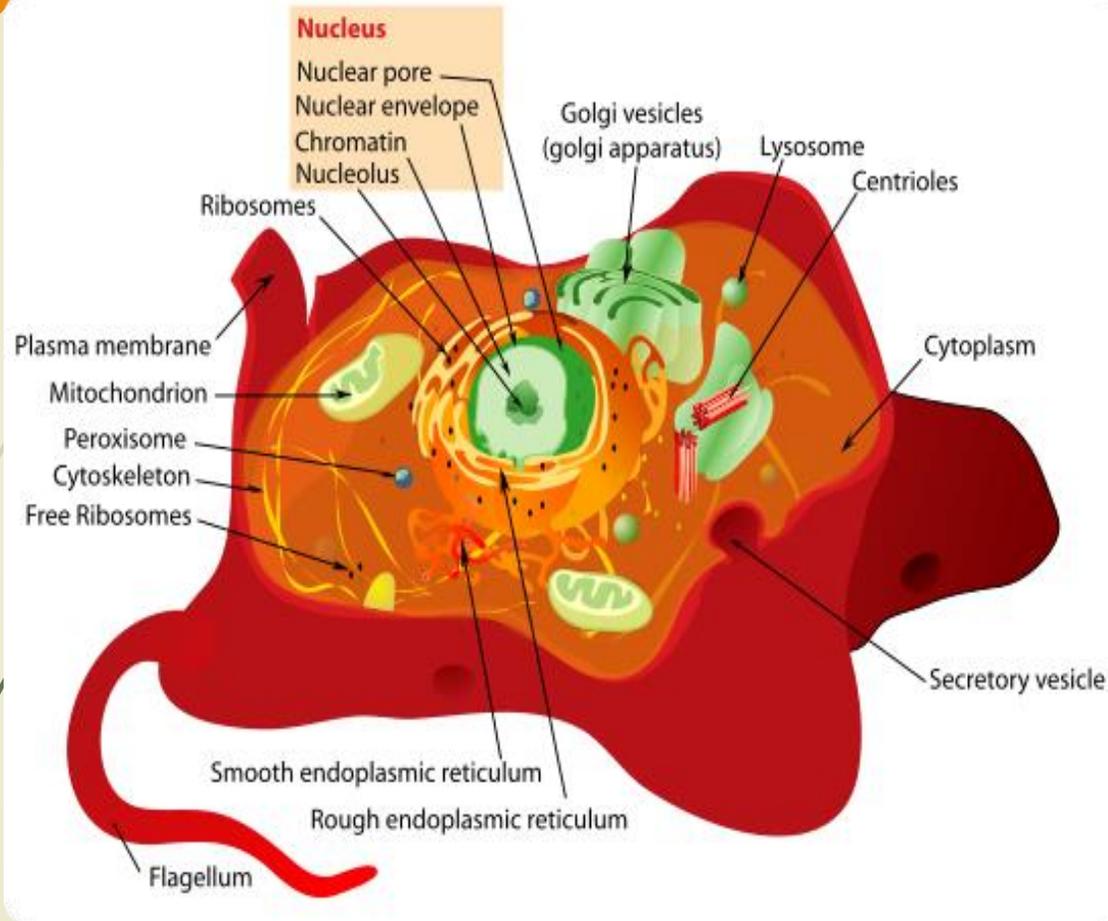
studij biologije i kemije



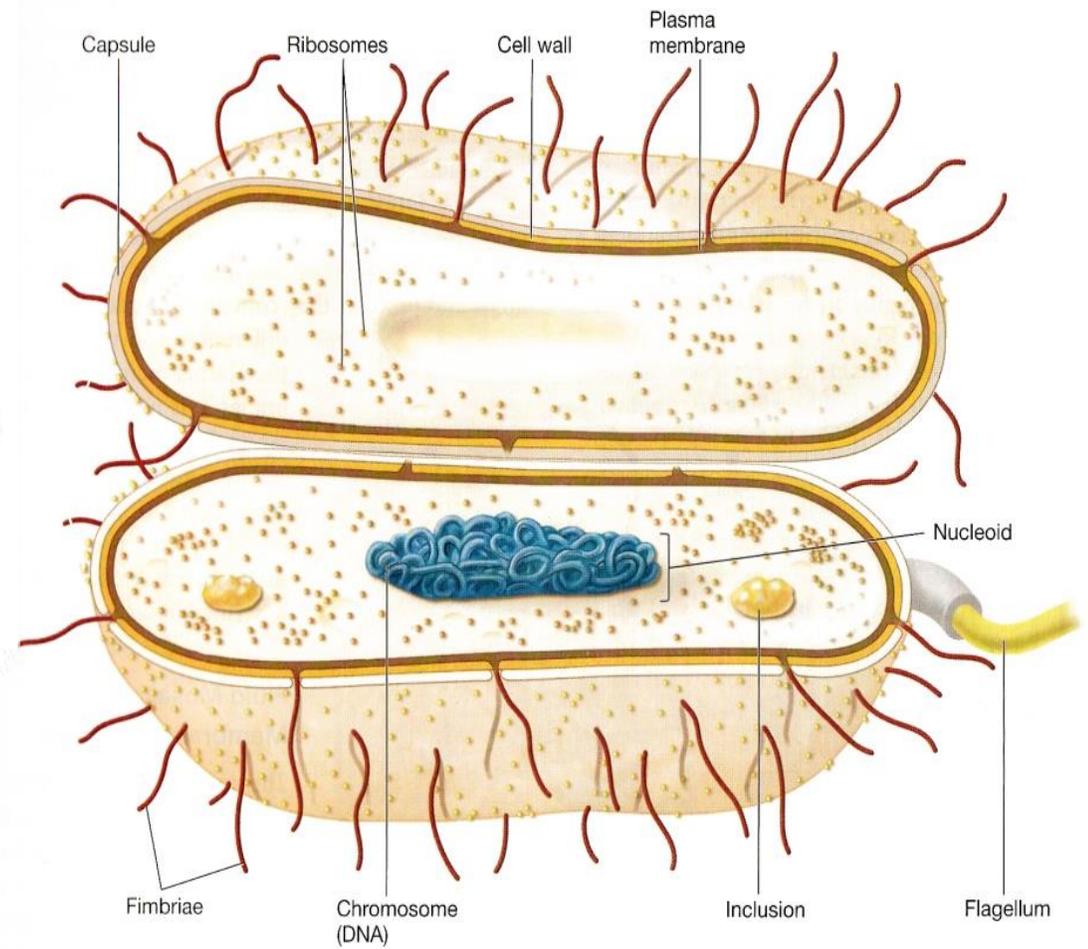
I. UNUTRAŠNJE STRUKTURE BAKTERIJSKIH STANICA



Eukariotska stanica



Bakterijska stanica



Zajedničke strukture bakterija i arheja i njihove funkcije

Plazma-membrana

- selektivno-propusna barijera, mehanička zaštita stanice, transport hranjivih i otpadnih tvari, mjesto odvijanja mnogih metaboličkih procesa (respiracija, fotosinteza), detekcija okolišnih čimbenika za kemotaksiju

Ribosomi

- sinteza proteina

Uklopine (inkluzije)

- skladištenje ugljika, fosfata i ostalih tvari

Nukleoid

- lokalizacija genetičkog materijala (DNA)

Periplazmatski prostor

- sadrži enzime za hidrolizu i vezne proteine za procesiranje i uzimanje hranjivih tvari

Stanična stijenka

- daje bakterijama oblik i služi zaštiti od stanične lize

Kapsule

- otpornost na fagocitozu, prihvaćanje za površine

Fimbrije i pili

- vezanje na površine, bakterijsko parenje

Flagele

- pokretanje

Endospore

- opstanak u nepovoljinim okolišnim uvjetima; samo kod bakterija



Citoplazma

Uklopine (inkluzije)

Unutarcitoplazmatske membrane

Ribosomi

Nukleoid



CITOPLAZMA

- **citoplazmatski matriks** – tvar koja se nalazi unutar plazma-membrane
- 75-98% sadržaja čini voda
- nema organela obavijenih membranom
- veće strukture u citoplazmi su: **nukleoid, ribosomi i uklopine pričuvnih tvari**
- **bakterijski citoskeleton** – sustav proteina nalik citoskeletonu eukariota - homolozi aktina, tubulina i intermedijarnih filamenata eukariota, ali i specifični proteini

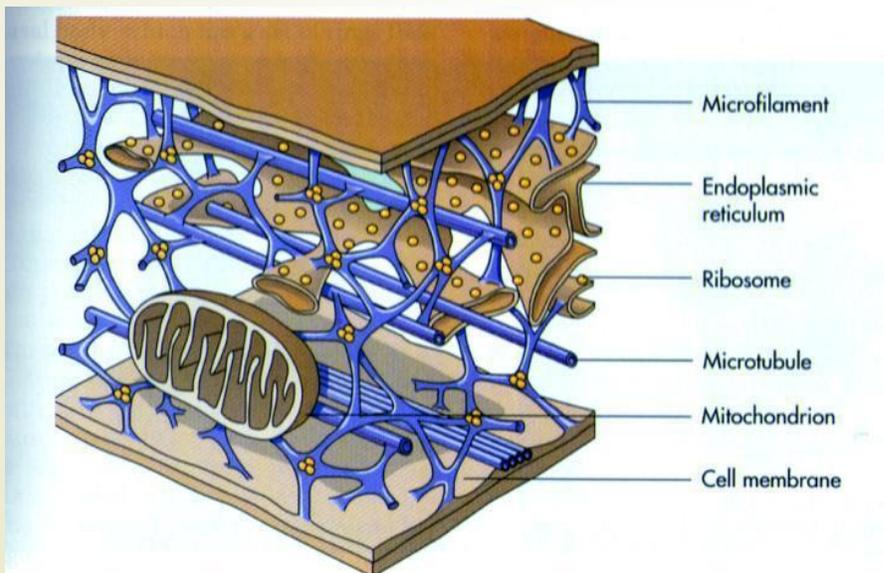
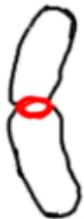
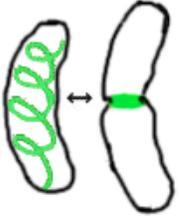
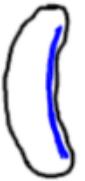


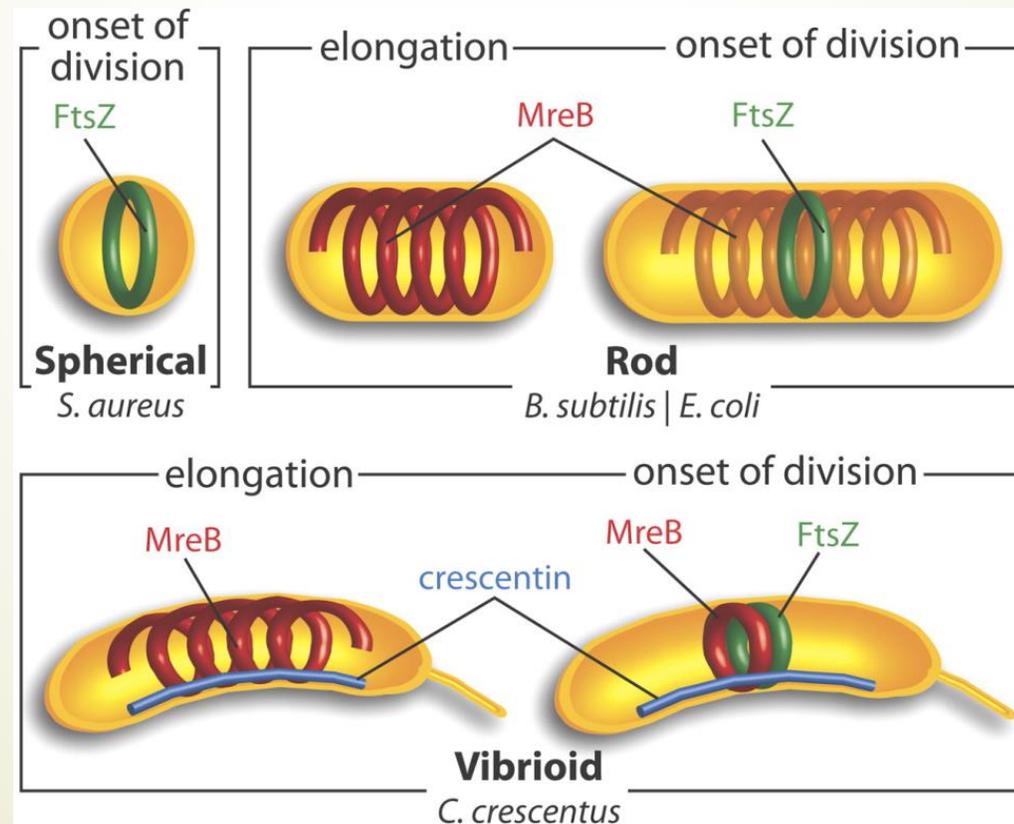
Fig. 3-43 Cytoskeleton. The cytoskeleton is a complex network that links the organelles of the eukaryotic cell. Organelles are attached to microfilaments of the cytoskeleton.

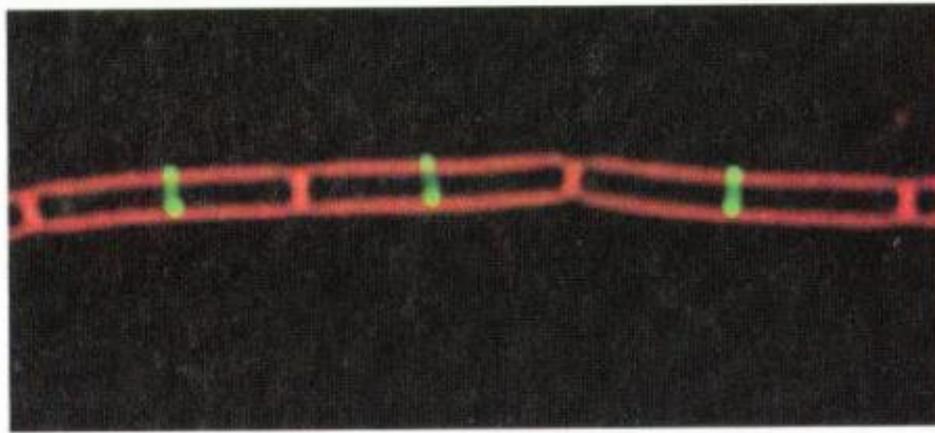
	Division	Polarity	Shape
Eukaryotes	Tubulin	Actin	Intermediate filaments
Prokaryotes	FtsZ	MreB	CreS
<i>Caulobacter</i> localization			

Skin and bones: the bacterial cytoskeleton, cell wall, and cell morphogenesis

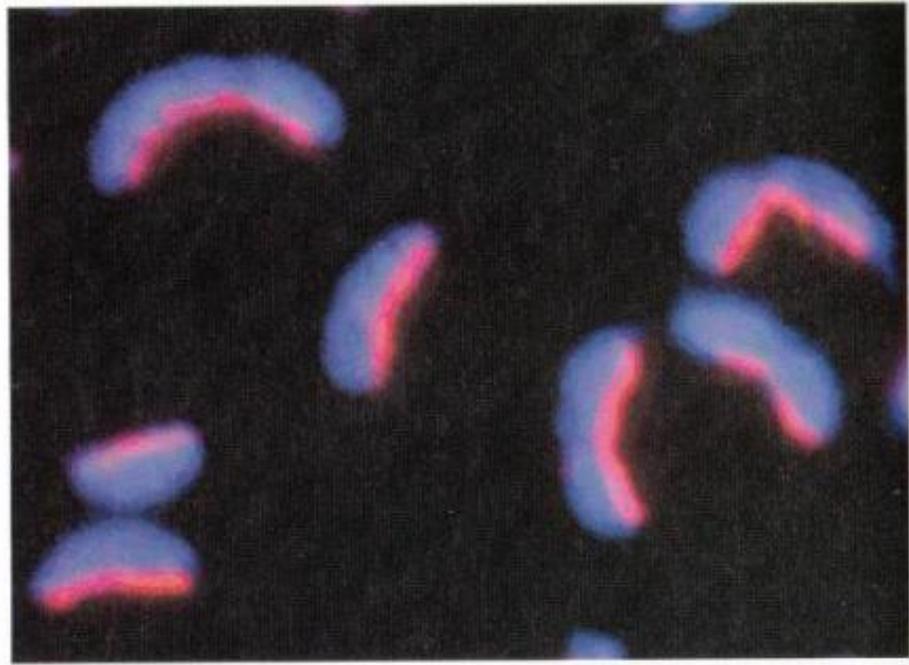
Matthew T. Cabeen and Christine Jacobs-Wagner

Department of Molecular, Cellular, and Developmental Biology, Yale University, New Haven, CT 06520





FtsZ protein (zeleno) bakterije *Bacillus subtilis*



CreS protein (crveno) bakterije *Caulobacter crescentus*

The bacterial cell division proteins FtsA and FtsZ self-organize into dynamic cytoskeletal patterns

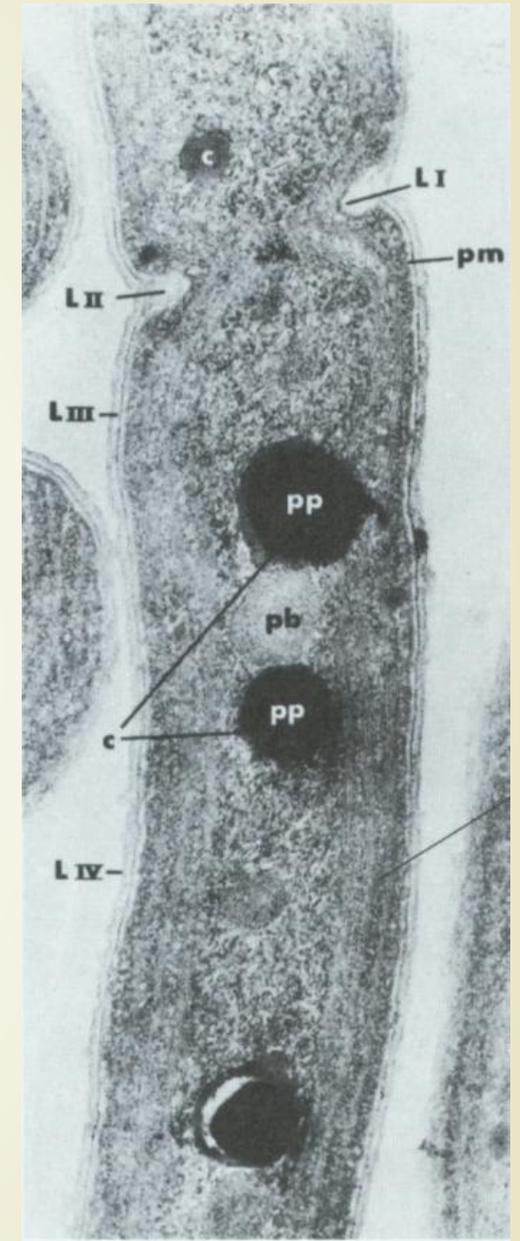
Martin Loose^{1,2} and Timothy J. Mitchison¹

<http://www.nature.com/ncb/journal/v16/n1/extref/ncb2885-sv6.mov>

<https://www.youtube.com/watch?v=y44dB2yC5Oo>

UKLOPINE ILI INKLUZIJE

- nakupine **organskog** ili **anorganskog** materijala, često jasno vidljive svjetlosnim mikroskopom
- **uloga** – pohrana pričuvnih tvari te smanjene osmotskog tlaka
- slobodno leže u citoplazmi (polifosfatna zrnca, zrnca glikogena) ili su obavijene jednostrukom membranom (zrnca sumpora, karboksisomi, plinske vakuole...)
- neke su u standardnom obliku zastupljene u svih bakterija, druge su ograničene na određene bakterijske vrste pa mogu biti osnova za identifikaciju
- različitog su sastava

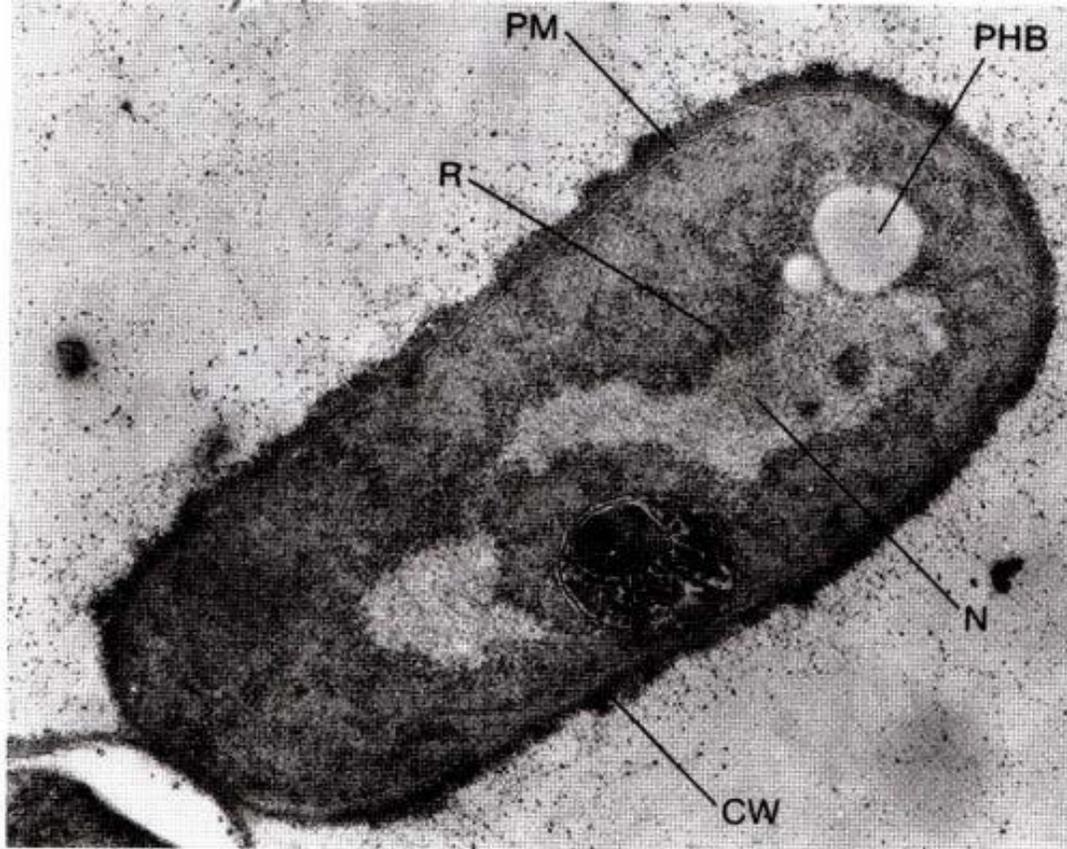


ORGANSKE UKLOPINE

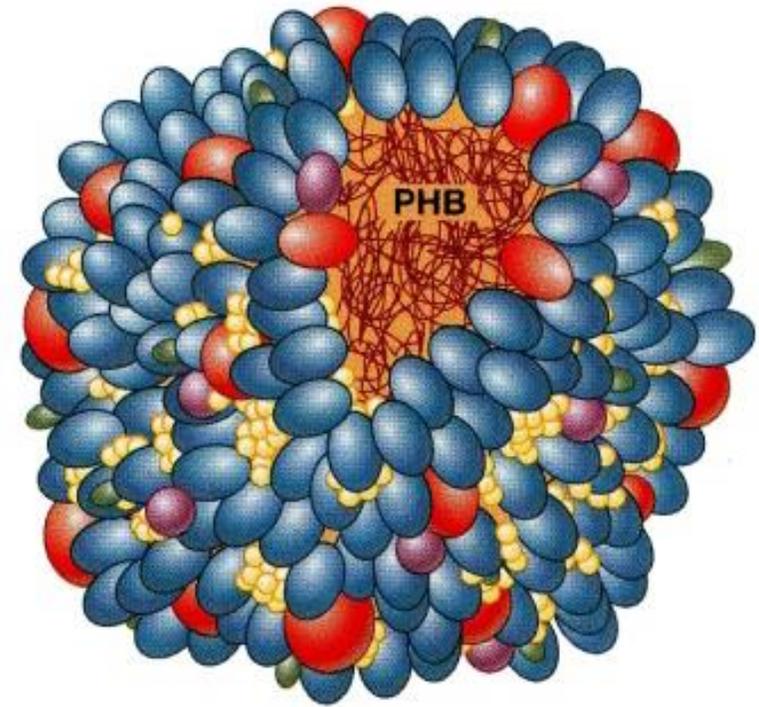
- **polisaharidna zrnca** – sadrže **glikogen** ili **škrob**, mogu se obojiti otopinom joda (zrnca glikogena crvenosmeđe, a zrnca škroba modro)
- uklopine **polihidroksibutirata (PHB)**
- zaliha ugljika



PHB-uklopine u bakterije roda *Vibrio*



(a)

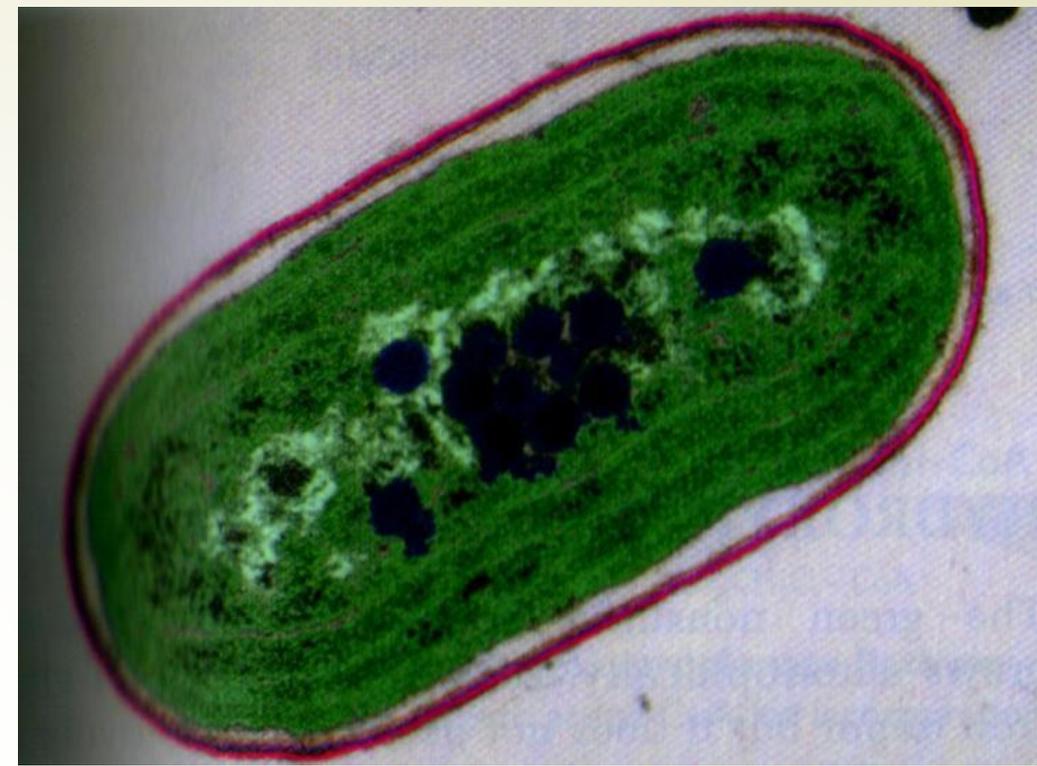


(b)

FIGURE 3.33 PHB Inclusions in Bacteria. (a) Electron micrograph of *Bacillus megaterium* ($\times 30,500$). PHB, poly- β -hydroxybutyrate inclusion; CW, cell wall; N, nucleoid; PM, plasma membrane; and R, ribosomes. (b) Structure of a PHB granule. PHB is enclosed by a membrane composed of several different proteins, including the PHB-synthesizing enzyme (red sphere) and the PHB-degrading enzyme (green sphere). Yellow spheres represent the phospholipids that are also found in the membrane. Note that the membrane is not a phospholipid bilayer.

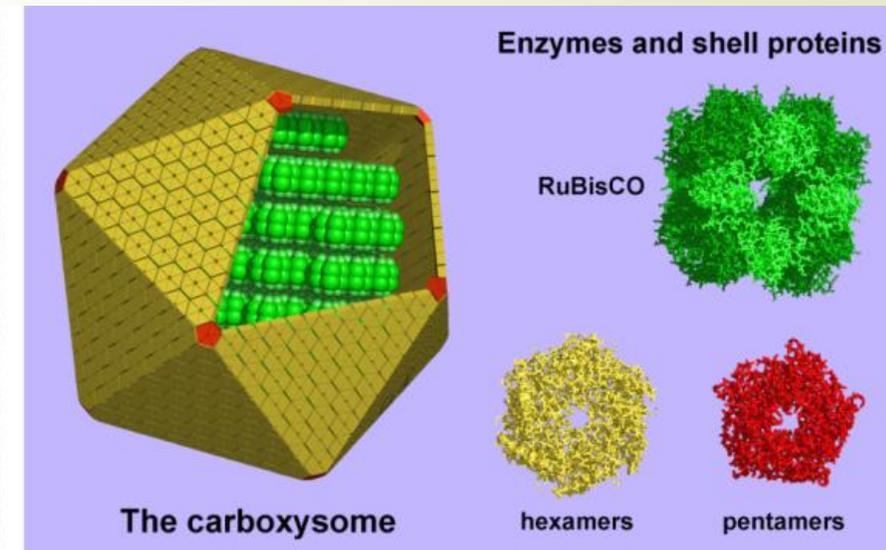
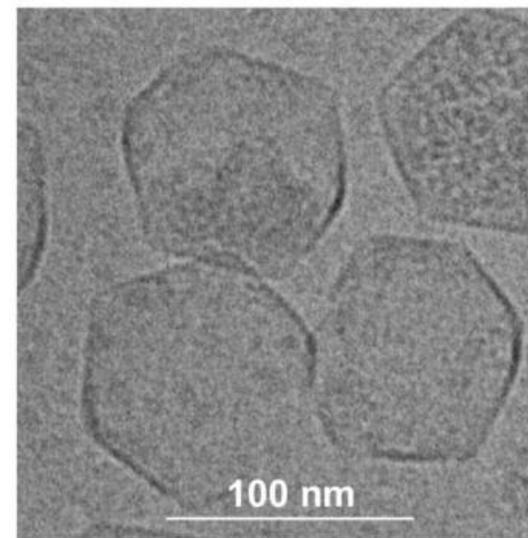
- polimeri koje je moguće koristiti za proizvodnju **biorazgradive plastike**

- **uklopine masti** (u obliku polimera hidroksimaslačne kiseline)
- **karboksisomi** - kod bakterija koje koriste CO_2 kao jedini izvor ugljika (cijanobakterije, nitrificirajuće bakterije); sadrže enzim uključen u prvi korak fiksacije ugljika tijekom fotosinteze – **RuBisco** – najzastupljeniji protein na Zemlji
- poliedri promjera oko 80-140 nm



Karboksisomi u cijanobakteriji *Synechococcus*

<https://www.youtube.com/watch?v=5NpHYr3bB2M>



- **plinske vakuole** (okružene proteinskom membranom, u mnogih vodenih prokariota) – omogućuju bakterijama plutanje na ili pri površini vode

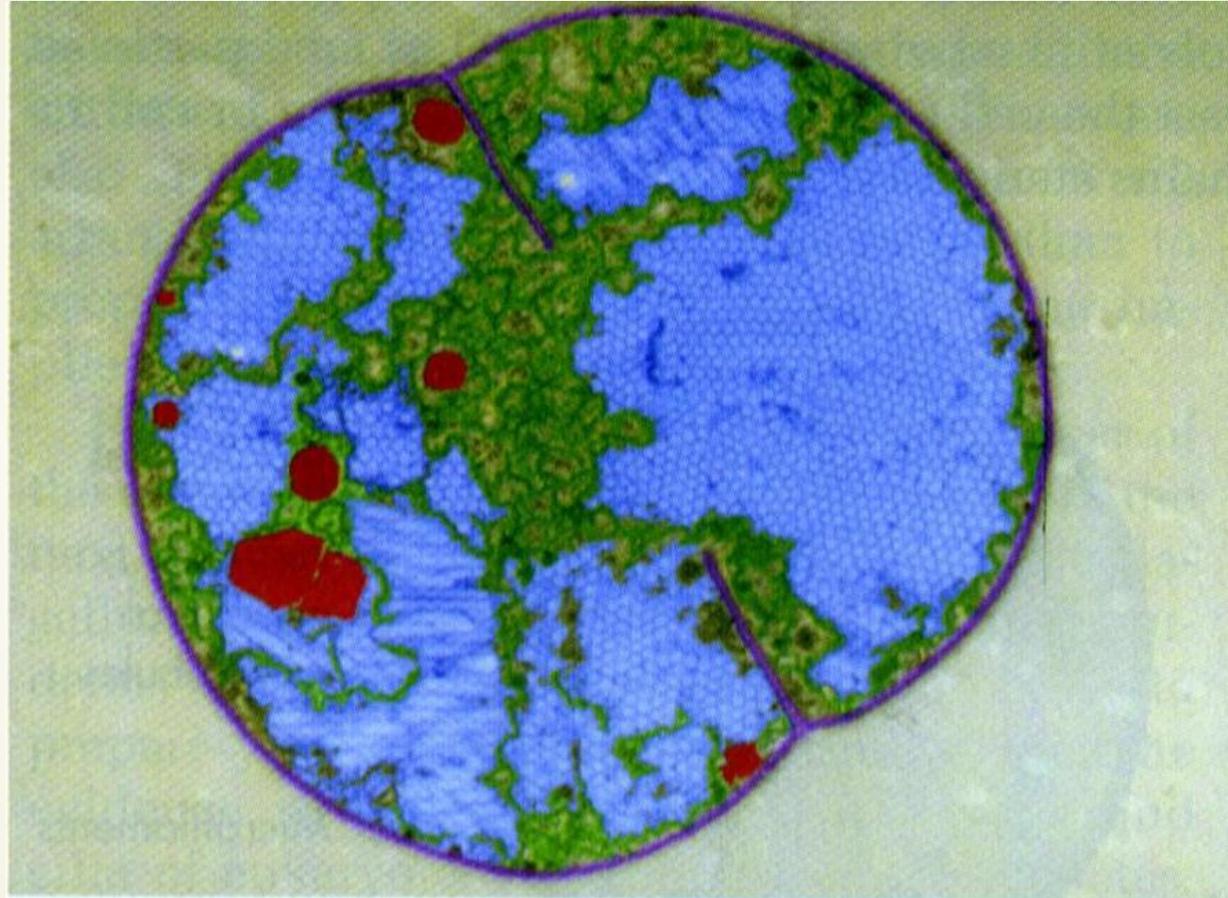


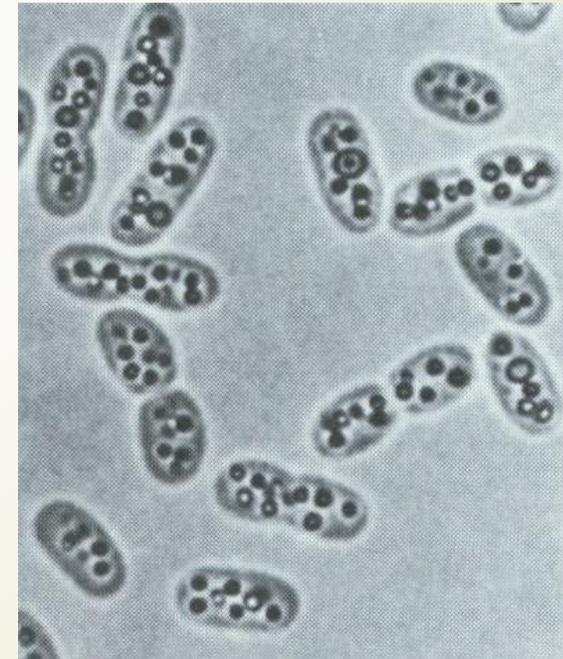
Fig. 3-50 Gas Vacuoles. Colorized micrograph of the gas vacuole (*blue*) and storage granules (*red*) of the cyanobacterium *Microcystis*. Changing the gas content of the gas vacuole permits this bacterium to adjust its buoyancy. (12,600 \times .)

ANORGANSKE UKLOPINE

- **polifosfatna zrnca** (metakromatska zrnca; volutin) – pričuva anorganskih fosfata koji mogu biti iskorišteni u sintezi ATP-a (karakterističnog su oblika u vrste *Corynebacterium diphtheriae* gdje predstavljaju dijagnostičku oznaku)
- **zrnca sumpora** (u “sumpornih bakterija” koje dobivaju energiju oksidacijom sumpora)

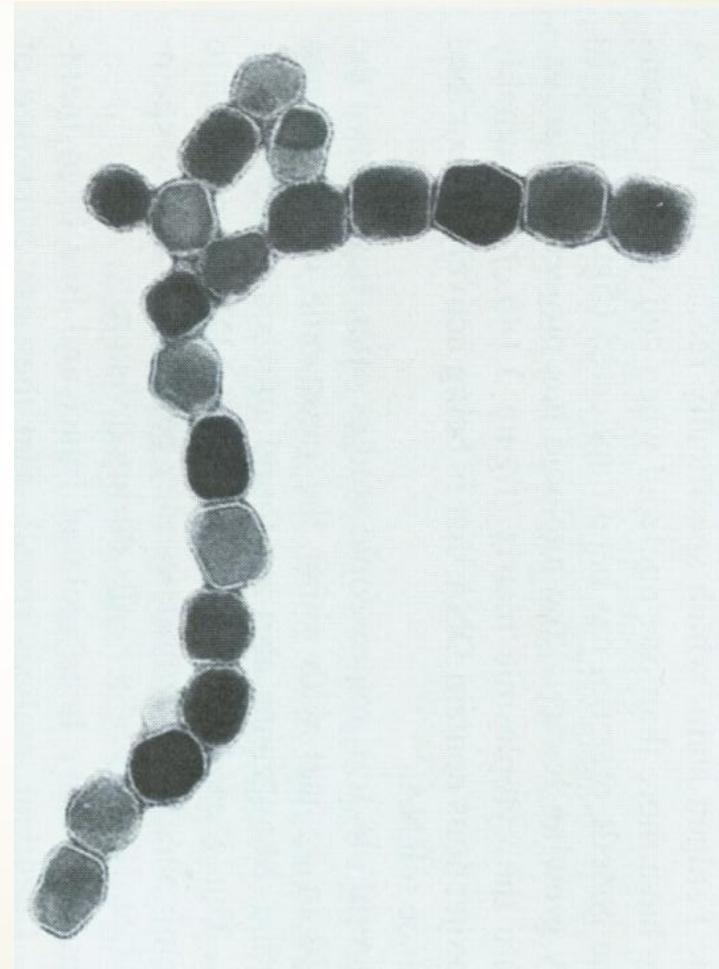
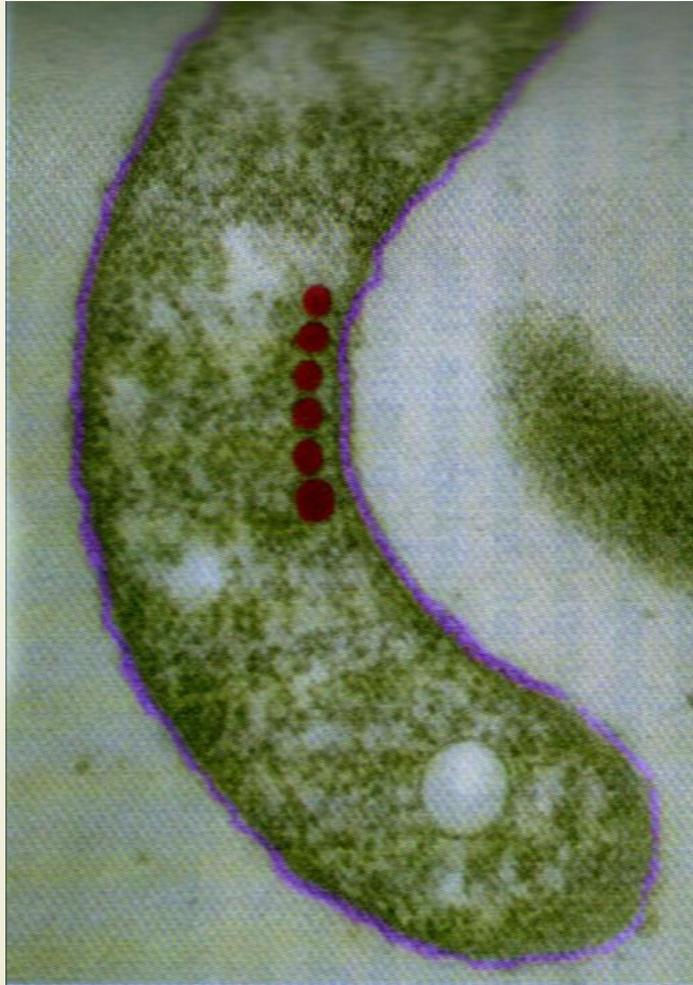


Polifosfatna zrnca u bakterije *Pseudomonas aeruginosa*

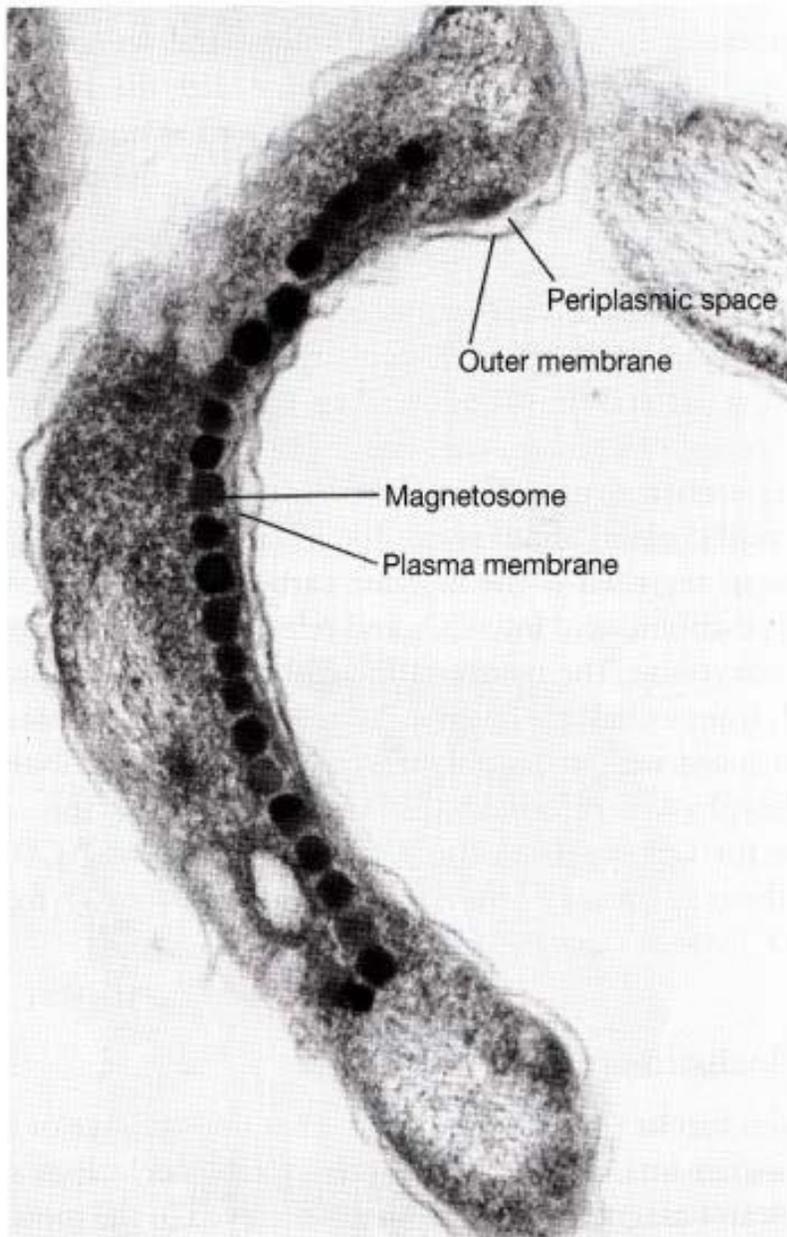


Zrnca sumpora u bakterije *Chromatium vinosum*

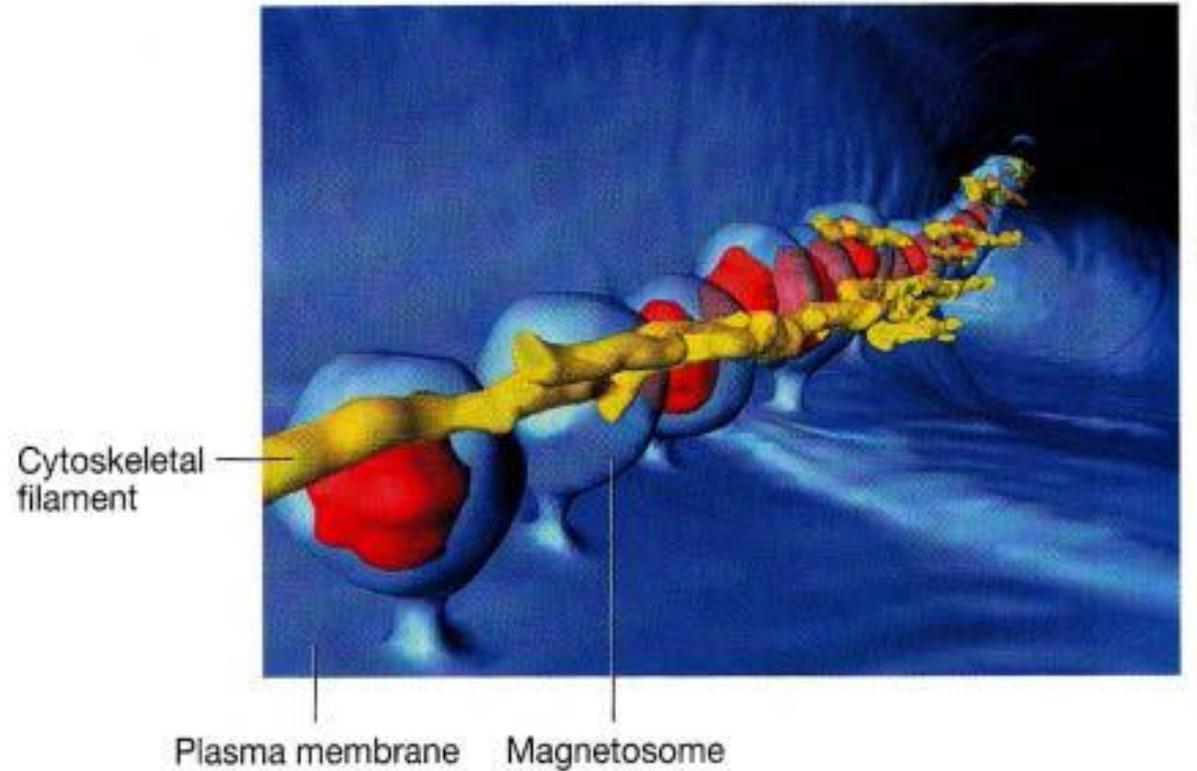
- **magnetosomi** – služe orijentaciji u Zemljinom magnetskom polju; uklopine promjera 40 do 100 nm okružene membranom; sadrže željezo u obliku magnetita (Fe_3O_4), greigita (Fe_3S_4) ili pirita (FeS_2) – imaju ih vodene magnetotaktične bakterije – “živi magneti”



Magnetosomi bakterije *Aquaspirillum magnetotacticum*



(a)



(b)

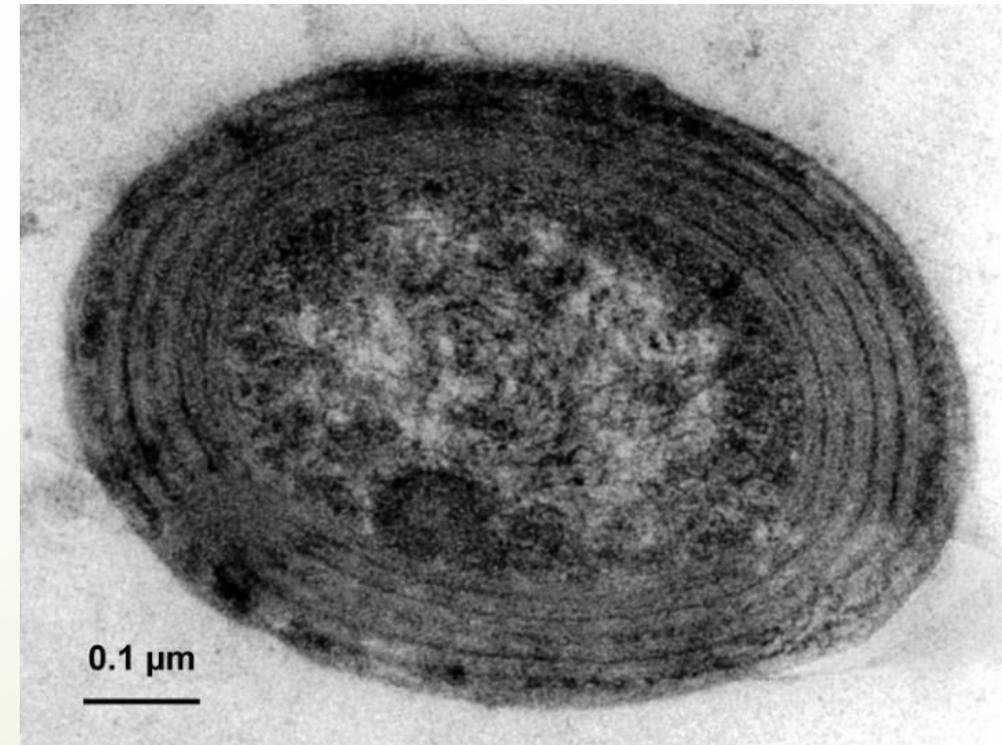
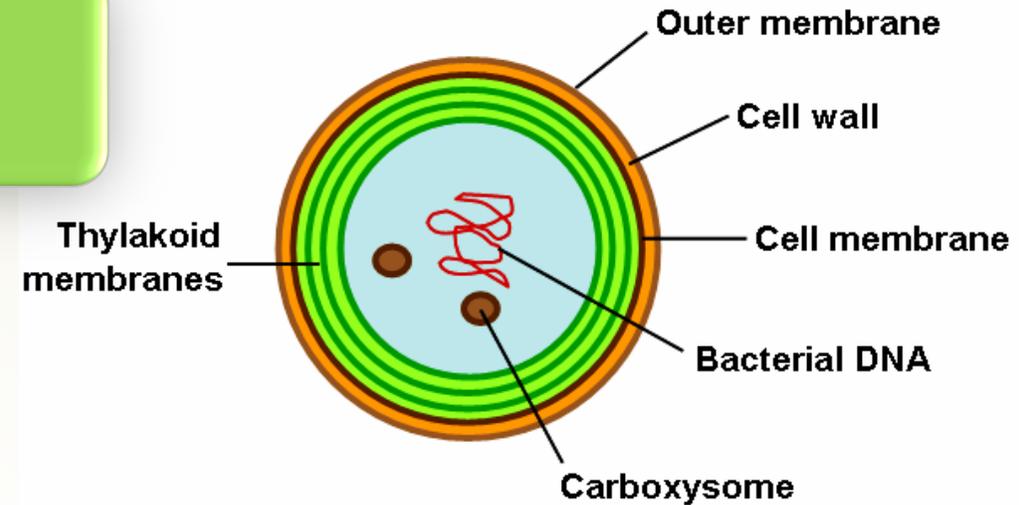
FIGURE 3.37 Magnetosomes. (a) Transmission electron micrograph of the magnetotactic bacterium *Aquaspirillum magnetotacticum* ($\times 123,000$). (b) An electron cryotomography three-dimensional reconstruction of the magnetosomes of *Magnetospirillum magneticum*.

<https://www.youtube.com/watch?v=3uUL4ooM6KI>

UNUTARCITOPLAZMATSKE MEMBRANE

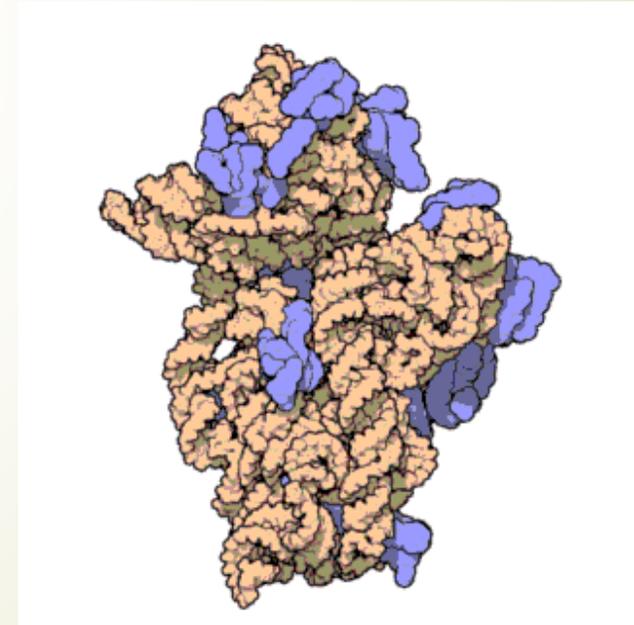
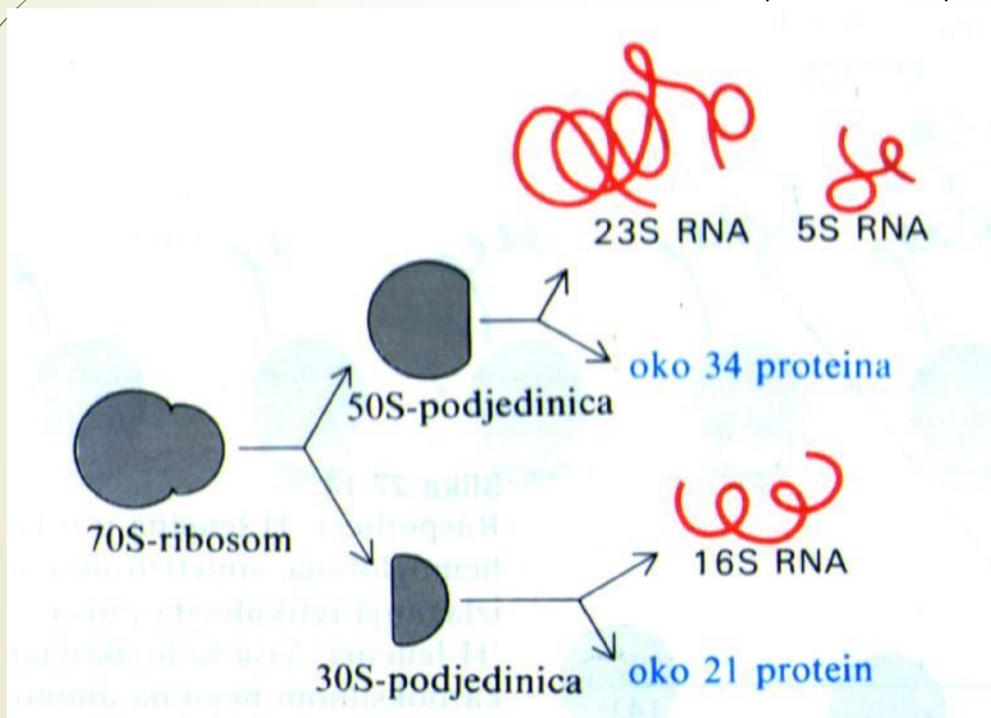
TILAKOIDI

- prisutni kod fotosintetski aktivnih bakterija – **cijanobakterija**
- u njima se odvija fotosinteza i respiracija
- funkcija – osigurati veću površinu membrana za veću metaboličku aktivnost
- **endosimbiontska teorija** – **kloroplasti** eukariotskih stanica su se razvili iz **cijanobakterija**



RIBOSOMI

- **kompleksi RNA i proteina** – sinteza proteina
- **manji su od eukariotskih ribosoma** (oko 20 nm) i nalikuju ribosomima mitohondrija i kloroplasta eukariotskih stanica
- 70S - ribosomi (S=Svedberg, jedinica za koeficijent sedimentacije)
- neki antibiotici (streptomycin, neomicin, tetraciklini) inhibiraju sintezu proteina na ribosomima bakterija ne djelujući na domaćinsku stanicu



Atomska struktura ribosomske podjedinice 30S bakterije *Thermus thermophilus*

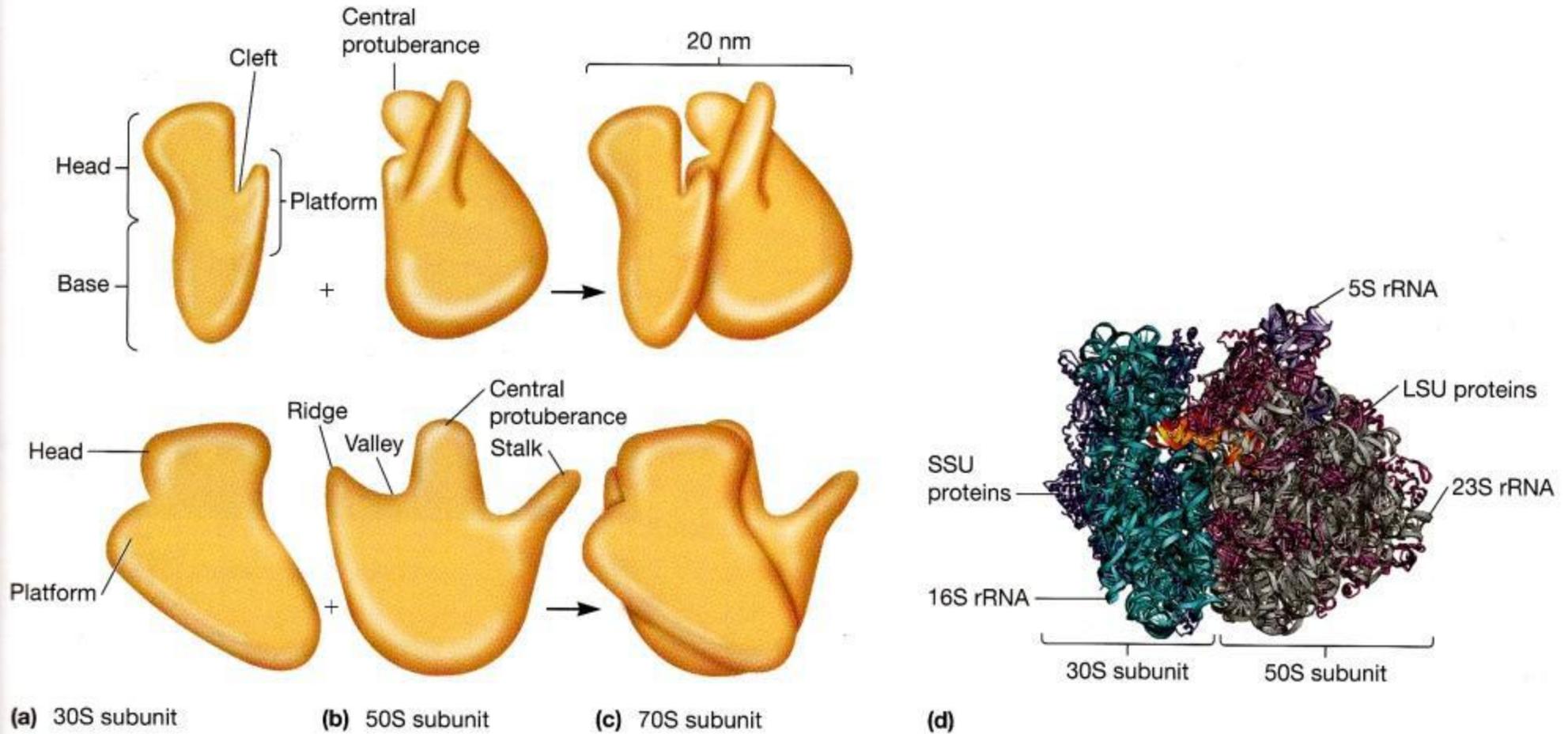
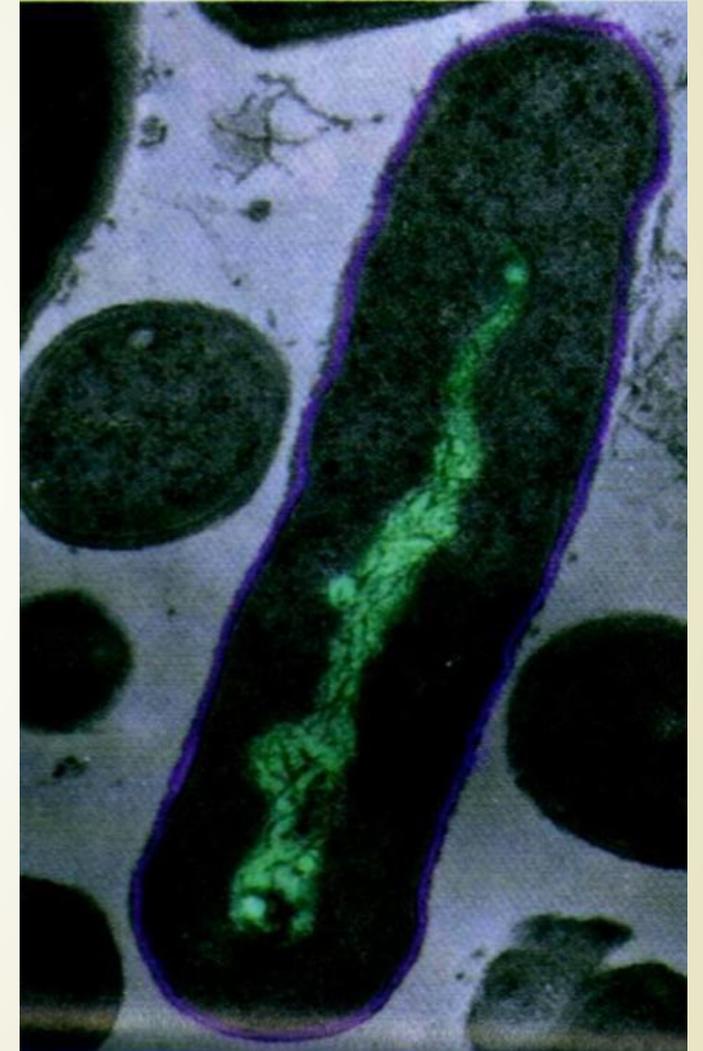


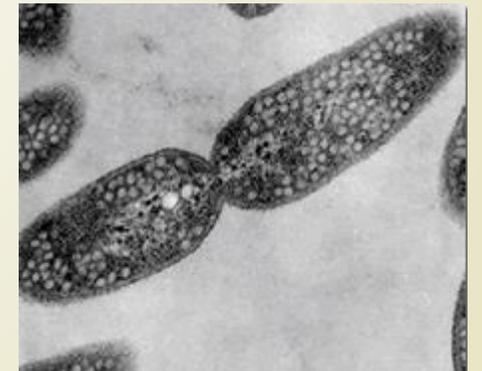
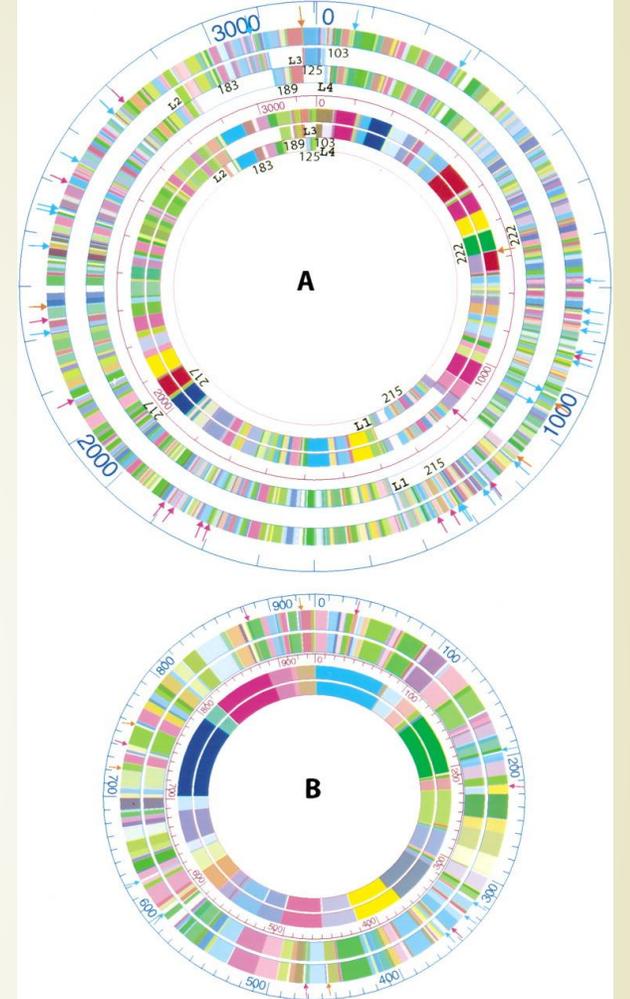
FIGURE 3.38 Bacterial Ribosomes. (a–c) Schematic representation of the two subunits and the complete 70S ribosome of *Escherichia coli*. (d) The molecular structure of the 70S ribosome of *Thermus thermophilus*. The 50S subunit (LSU) includes 23S rRNA (gray) and 5S rRNA (lavender), while 16S rRNA (turquoise) is found in the 30S subunit (SSU). A molecule of tRNA (gold) is shown in the A site. To generate this ribbon diagram, crystals of purified bacterial ribosomes were grown, exposed to X rays, and the resulting diffraction pattern analyzed.

NUKLEOID

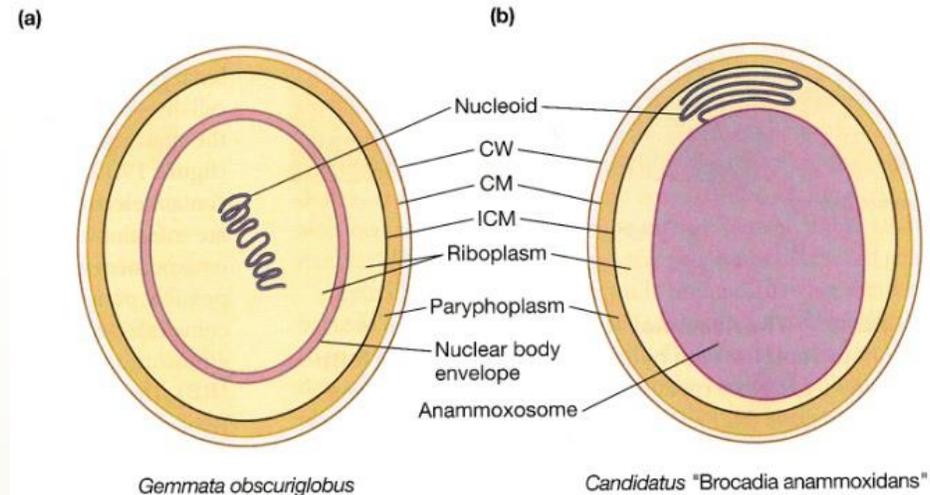
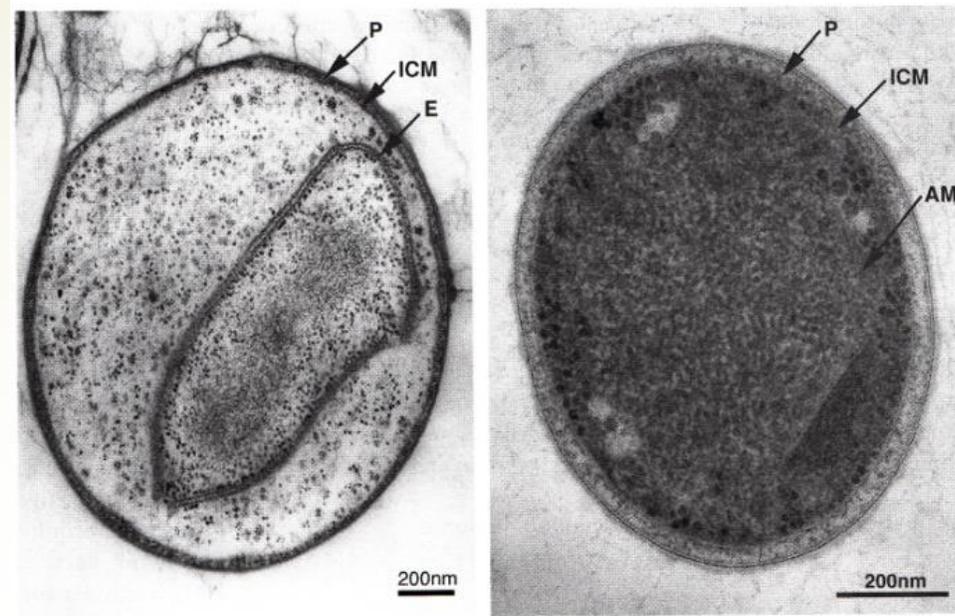
- jezgrin ekvivalent u stanicama bakterija i arheja
- **nukleoid** - bakterijski kromosom ne sadrži histone i nije obavijen jezgrinom membranom, dok neke arheje imaju nukleosome, odnosno histone
- nukleoid je nepravilnog oblika, ali može biti i kuglast, izdužen ili u obliku bučica za vježbanje
- čini ga obično **kružna dvolančana molekula DNA** koja sadrži kompletnu genetičku informaciju nužnu za strukturu i funkciju stanice



- postoje i bakterije s **linearnim kromosomom** (neke vrste iz roda 'Candidatus Phytoplasma', neke spirohete iz roda Borelia, rod Streptomyces)
- postoje bakterije s **višestrukim (multiplim) kromosomima** – kombinacije kružnih i linearnih ili više kružnih kromosoma
- *Rhodobacter sphaeroides*, *Agrobacterium tumefaciens*, *Deinococcus radiodurans*, *Vibrio cholerae*, rod *Brucella*, rod *Bulkholderia*...
- **veličina genoma** – od samo 160 kbp kod nekih endosimbiotskih bakterija do 12 200 kbp kod nekih bakterija iz tla



- *Planctomycetes* – imaju genetički materijal obavijen membranom



(c)

FIGURE 19.10 Planctomycete Cellular Compartmentalization. (a) An electron micrograph of *Gemmata obscuriglobus* showing the nuclear body envelope (E), the intracytoplasmic membrane (ICM), and the paryphoplasm (P). (b) An electron micrograph of the anaerobic ammonia-oxidizing planctomycete *Candidatus "Brocadia anammoxidans"*. The anammoxosome is labeled AM. (c) Schematic drawings corresponding to (a) and (b): cell wall (CW), cytoplasmic membrane (CM).



PLAZMIDI

Bakterijska DNA

plazmidi



- male kružne molekule dvolančane DNA (izvankromosomski genetički elementi)
- različitih su veličina (1 do 200 kbp), prisutni u različitom broju kopija kod pojedinih bakterijskih vrsta, repliciraju se neovisno o kromosomskoj DNA
- mehanizam replikacije – sigma i theta replikacija
- genetska informacija koju sadrže nije odlučujuća za preživljenje u normalnim uvjetima
- mogu nositi gene za otpornost na antibiotike, toleranciju prema toksičnim metalima, sintezu vlastitih toksina, sintezu nekih enzima, svojstvo konjugacije, patogenost
- genetičko inženjerstvo – plazmidi kao vektori

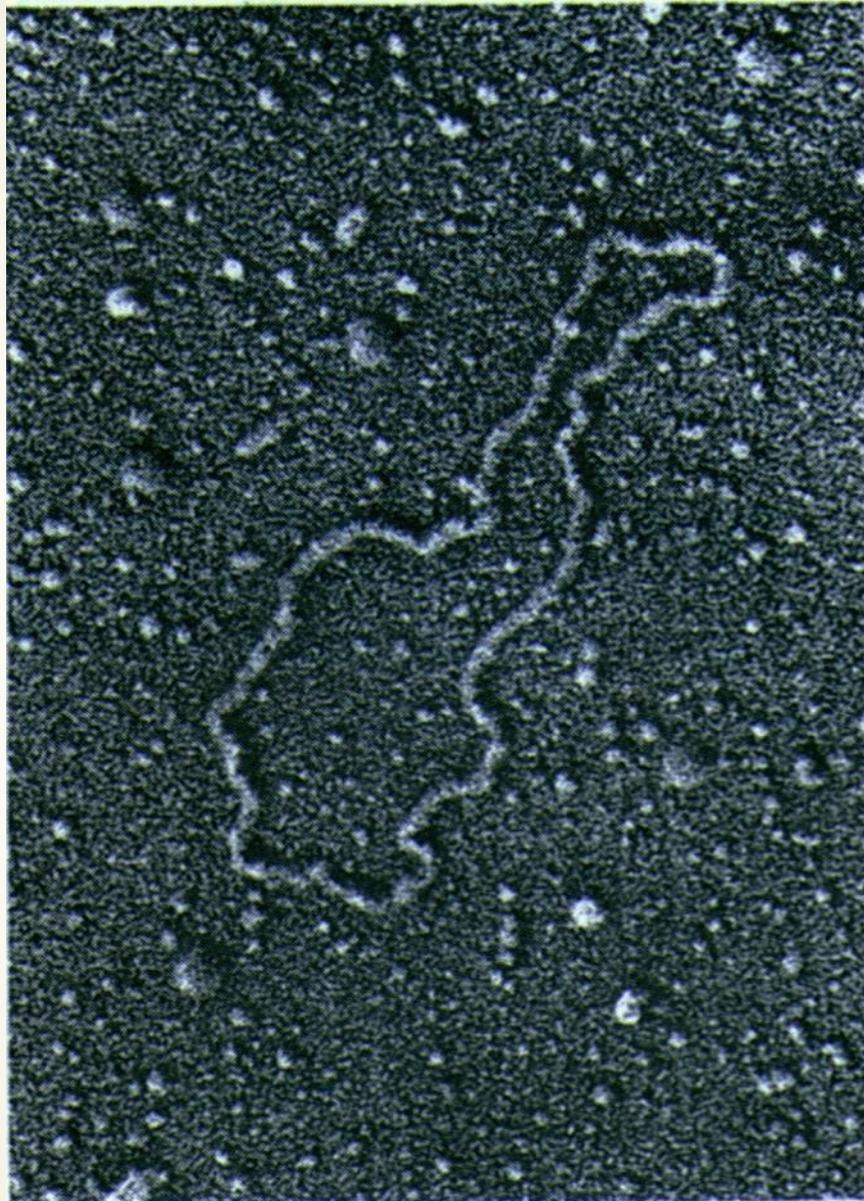
Glavni tipovi plazmida:

Bakterijska DNA

plazmidi

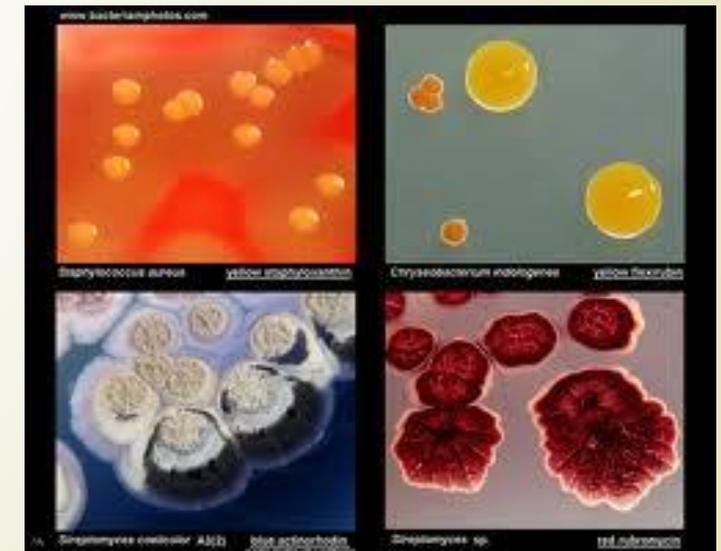


- **konjugacijski plazmidi** – F-faktor – konjugacija
- **R- plazmidi** – RP₄, pSH6 – konjugacija, otpornost na antibiotike
- **Col-plazmidi** – geni za bakteriocine – npr. *ColE1* – proizvodnja kolicina E₁
- **plazmidi nositelji virulencije** – pretvaraju bakteriju u patogena – npr. Ent; Ti – proizvodnja enterotoksina; indukcija tumora u biljaka
- **metabolički plazmidi** – CAM, TOL – degradacija kamfora; degradacija toluena



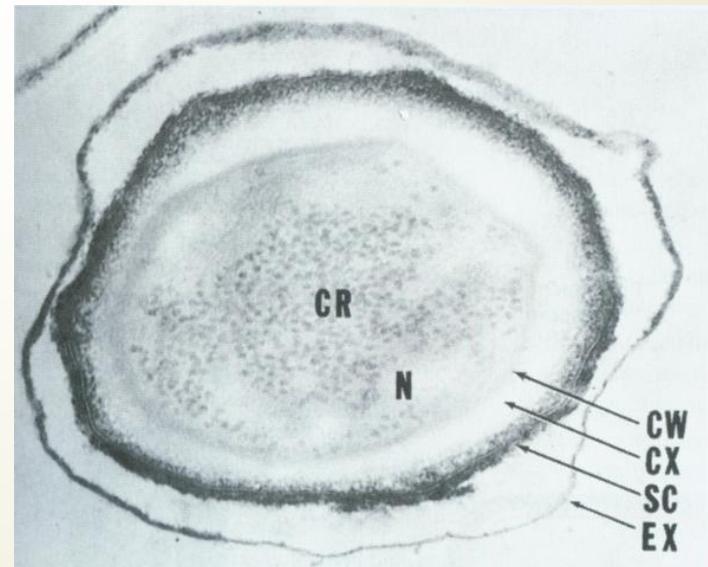
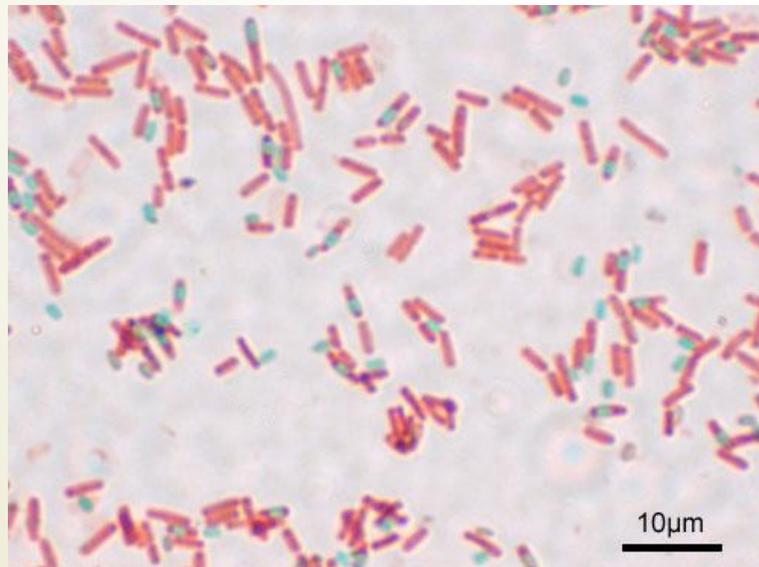
PIGMENTI

- sporedni produkti metabolizma (sekundarni metaboliti)
- karotenoidi, klorofil...
- zaštićuju stanicu od djelovanja ultraljubičastog i vidljivog svjetla
- mnoge pigmentirane bakterije sintetiziraju antibiotike i druge antimikrobne tvari
- sposobnost sinteze pigmenta genetički je uvjetovana i predstavlja značajku bakterijske vrste

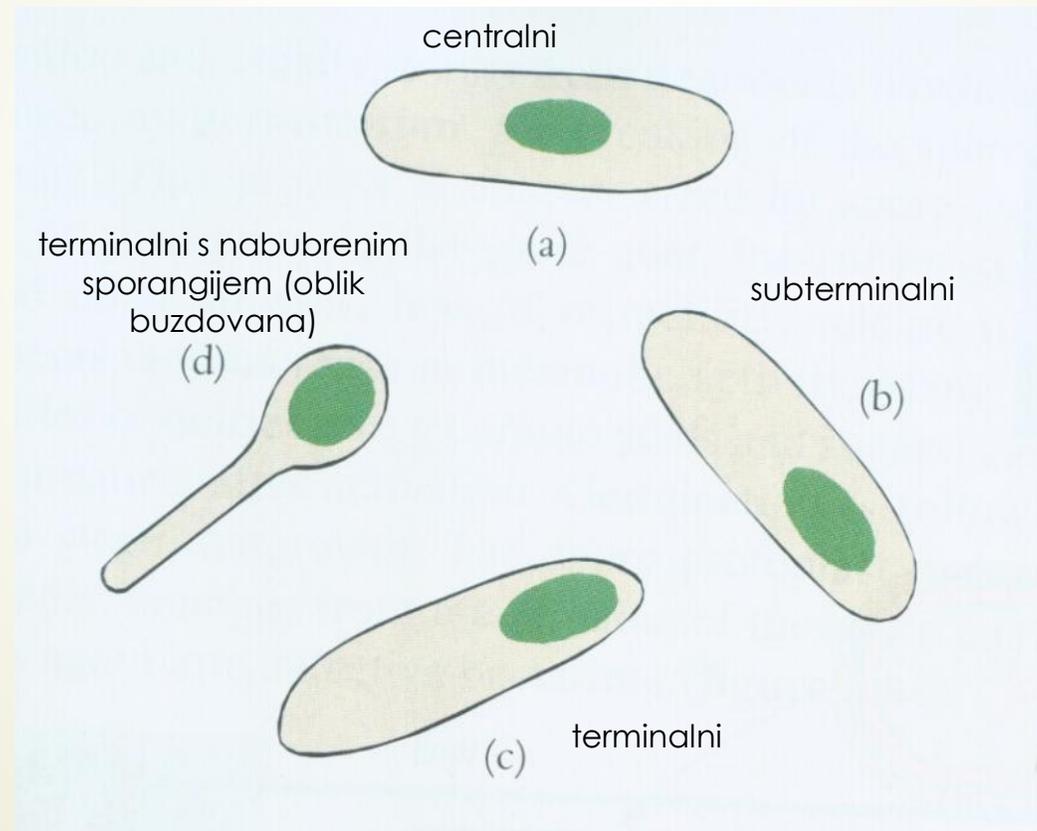


ENDOSPORE

- nastaju unutar vegetativnih bakterijskih oblika u nepovoljnim životnim uvjetima (nedostatak vode ili hrane) – **opstanak**
- nisu reproduktivne strukture
- mogu ih stvarati neke bakterije (sporogene – *Bacillus*, *Clostridium*, *Desulfotomaculum*, *Sporosarcina*, *Sporolactobacillus*, *Oscillospira* i *Thermoactinomyces*) dok druge ne mogu (asporogene)
- otporne na UV-zračenje, γ -zračenje, isušivanje, dezinfekcijska sredstva



- **oblik endospora** (okrugao ili ovalan), položaj u stanici (centralni, subterminalni, terminalni) te promjer u odnosu na promjer bakterijske stanice (manji, jednak, veći) za određenu su bakterijsku vrstu stalne odlike



Endospore su uključene u prijenos nekih oboljenja na čovjeka.

Infekcije prenošene na čovjeka preko endospora :

- **antraks** - *Bacillus anthracis*
- **tetanus** - *Clostridium tetani*
- **botulizam** - *Clostridium botulinum*
- **plinska gangrena** - *Clostridium perfringens*

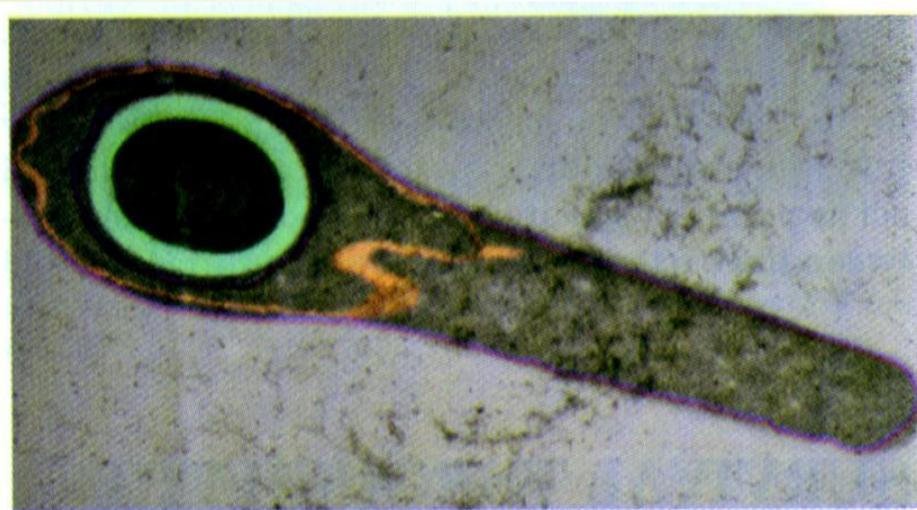


Fig. 3-57 Sporulation—Formation of Bacterial Endospores. A. The formation of an endospore.

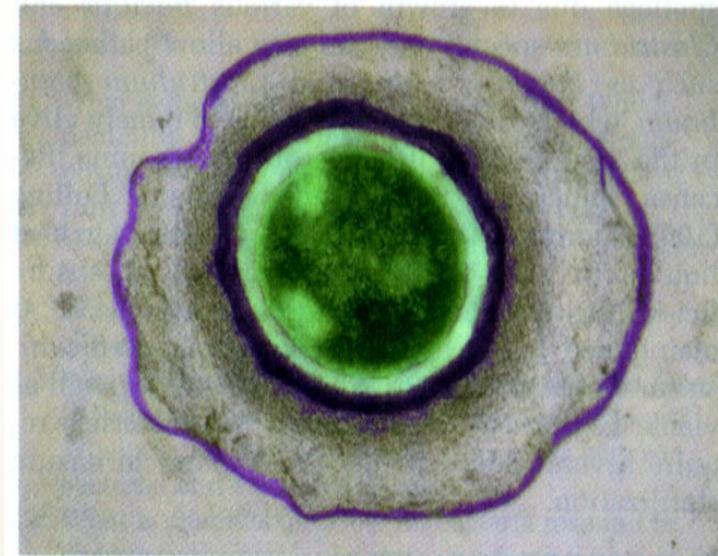
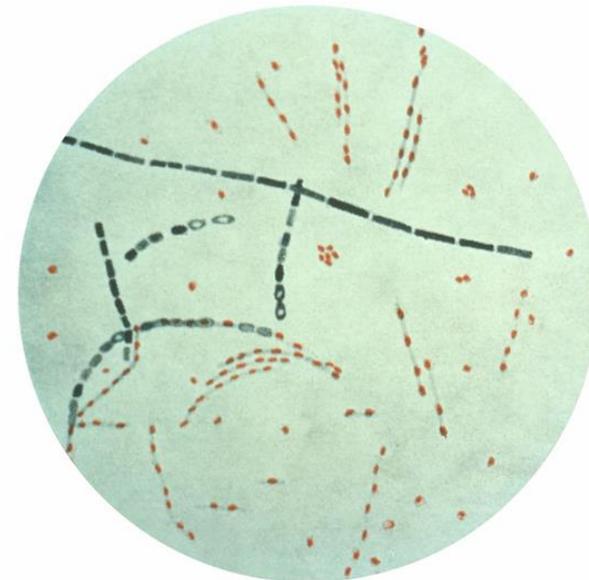
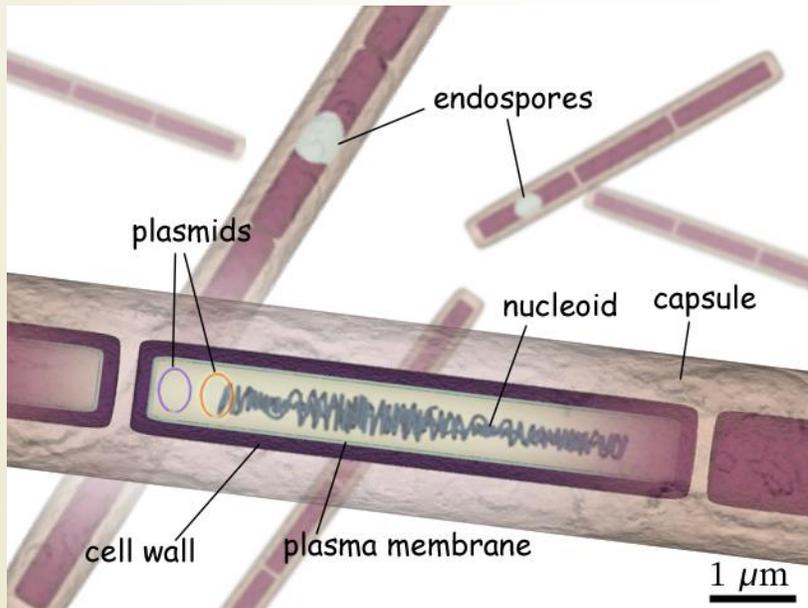


Fig. 3-57 Sporulation—Formation of Bacterial Endospores. B. The mature endospore.

Izraziti primjer otpornosti : endospore bakterije *Bacillus anthracis*

- preživljavaju 10 minuta pri 180°C
- preživljavaju u suhom mediju više od 60 godina
- smrtonosne koncentracije dezinfekcijskih sredstava veće su do 100 000 puta nego pri uništavanju vegetativnih stanica





Sporulacija (proces nastajanja spora) traje nekoliko sati

- plazma-membrana urasta oko tek repliciranog bakterijskog kromosoma i malo citoplazme tvoreći septum spore
- plazma-membrana još jednom obavija sporu
- između dva sloja plazma-membrane ugradi se debeli sloj peptidoglikana
- oko vanjske membrane stvara se debeli proteinski omotač (odgovoran za otpornost prema mnogim kemijskim agensima)
- liziranjem vegetativne stanice oslobađa se zrela endospora

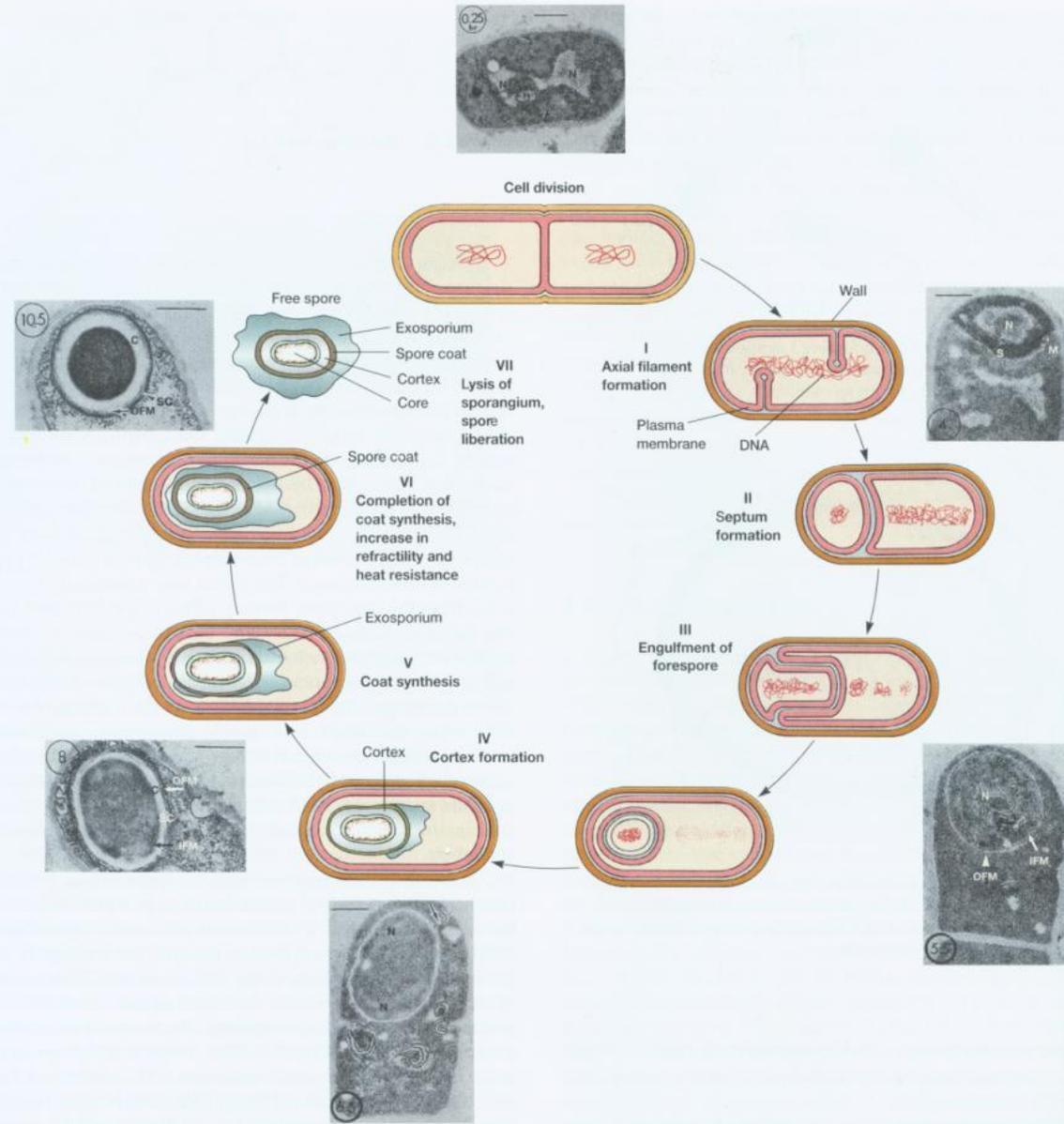


Figure 3.43 Endospore Formation: Life cycle of *Bacillus megaterium*. The stages are indicated by Roman numerals. The circled numbers in the photographs refer to the hours from the end of the logarithmic phase of growth: 0.25 h—a typical vegetative cell; 4 h—stage II cell, septation; 5.5 h—stage III cell, engulfment; 6.5 h—stage IV cell, cortex formation; 8 h—stage V cell, coat formation; 10.5 h—stage VI cell, mature spore in sporangium. Abbreviations used: C, cortex; IFM and OFM, inner and outer forespore membranes; M, mesosome; N, nucleoid; S, septum; SC, spore coats. Bars = 0.5 μm.

<http://www.youtube.com/watch?v=NAcowliknPs>

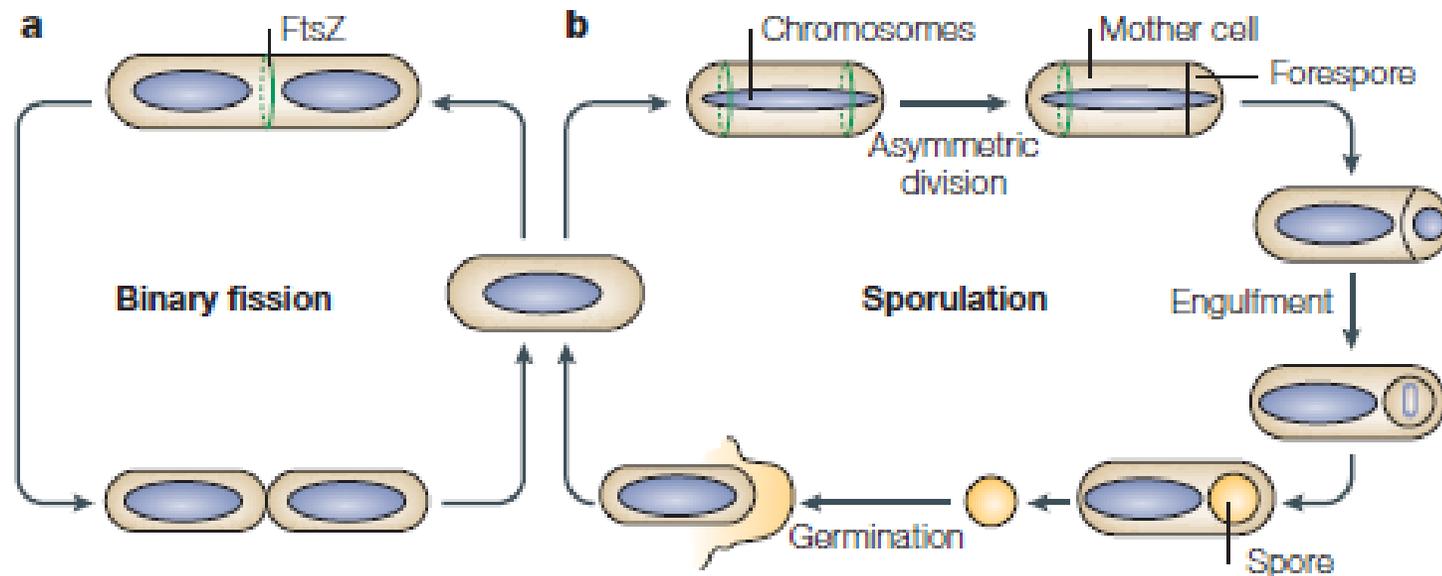
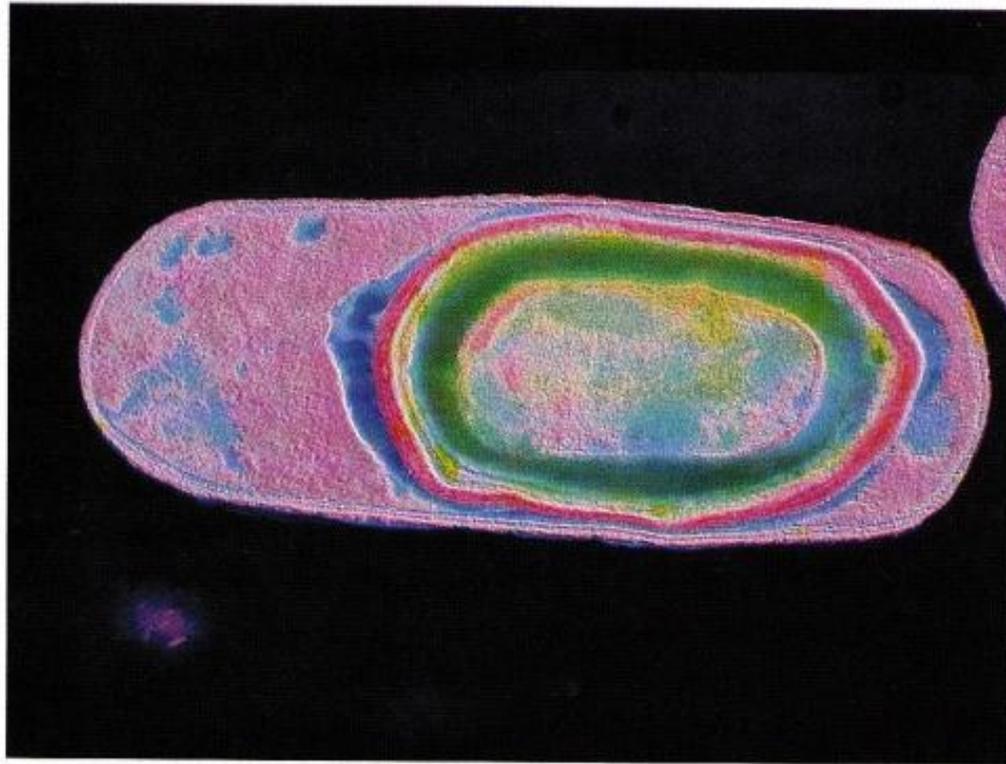
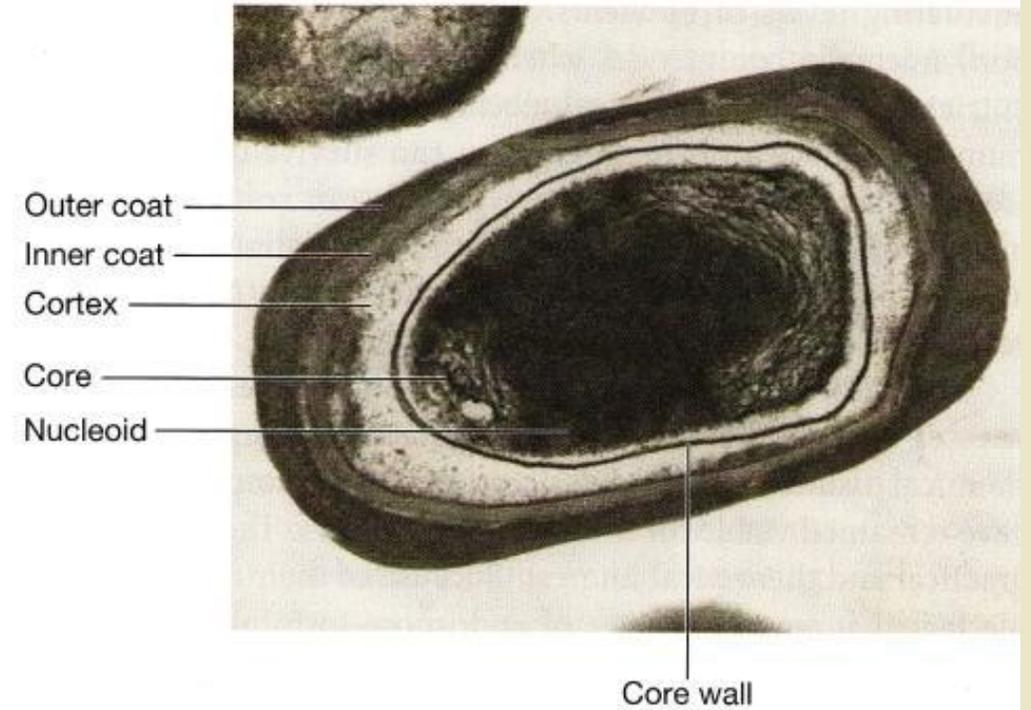


Figure 1 | Life cycles of *Bacillus subtilis*. *B. subtilis* has two alternative life cycles that result in different patterns of cell division. **a** | The vegetative life cycle. When conditions are favourable, *B. subtilis* elongates, replicates its chromosome (shown in blue) and divides by binary fission. The division apparatus assembles with FtsZ (green) in a ring-like structure at the midcell, where cell division occurs. **b** | When resources are exhausted, *B. subtilis* can develop a highly resistant and dormant cell to survive the harsh environmental conditions. The two copies of the chromosome adopt a novel configuration that stretches from one pole of the cell to the other. The division machinery assembles at both poles of the cell but cell division occurs at only one pole. A portion of one chromosome is trapped by the division septum. Proteins in the division septum package the chromosome into the smaller cell (known as the forespore). The forespore is then fully engulfed by the larger mother cell. Through the coordinate expression of genes in both cells, the internalized forespore is prepared for dormancy. Specialized proteins bind to and protect the DNA, the cell cytoplasm becomes mineralized and a protective protein barrier is assembled on the outer surface of the cell. When conditions improve, the endospore germinates and *B. subtilis* re-enters a vegetative life cycle.



(a)



(b)

FIGURE 3.52 Bacterial Endospores. (a) A colorized cross section of a *Bacillus subtilis* cell undergoing sporulation. The oval in the center is an endospore that is almost mature; when it reaches maturity, the mother cell will lyse to release it. (b) A cross section of a mature *B. subtilis* spore showing the cortex and spore coat layers that surround the core. The endospore in (a) is 1.3 μm ; the spore in (b) is 1.2 μm .

Germinacija – klijanje endospore pri ponovnom uspostavljanju povoljnih uvjeta za život

- aktiviranje litičkih enzima
- razaranje sporina omotača
- tvorba germinacijskog kanala za ulazak vode i hranjivih tvari
- aktiviranje metabolizma
- bujanje spore unutar sporina omotača, tvorba plazma-membrane i stijenke, izlazak vegetativne stanice iz sporina omotača

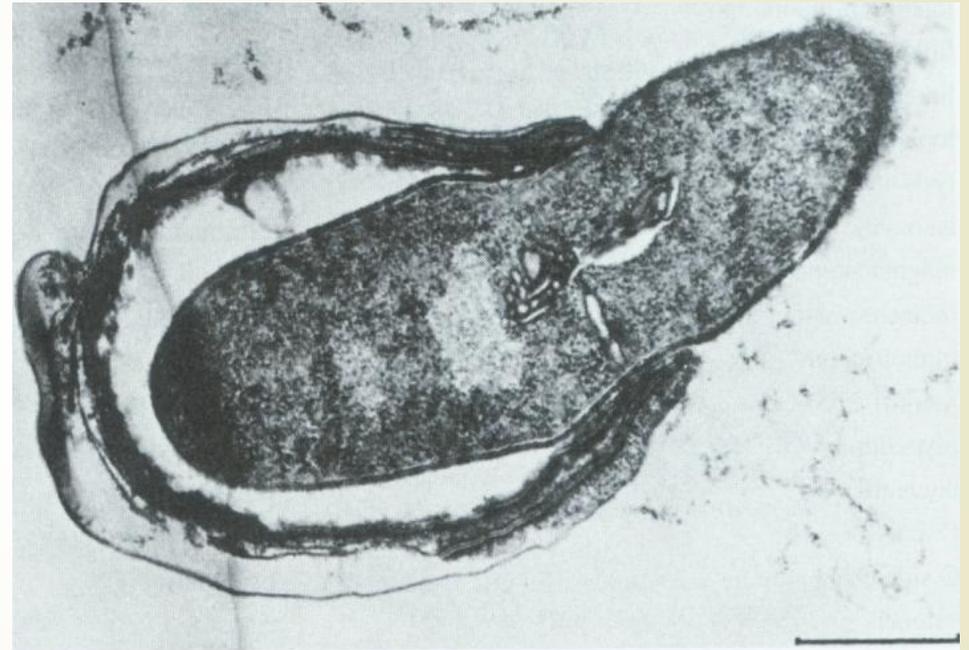
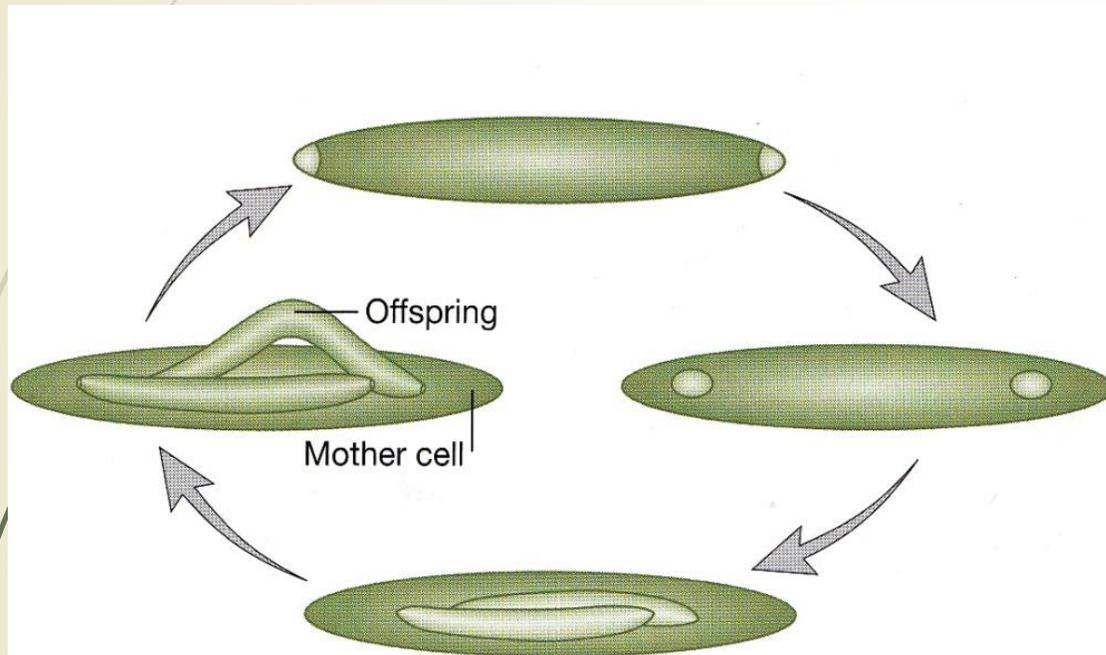


Figure 3.44 Endospore Germination. *Clostridium pectinovorum* emerging from the spore during germination. Bar = 0.5 μm .

Viviparnost u bakterija

- bakterije koje “imaju bebe”
- neobičan oblik sporulacije



Production of Intracellular Living Offspring by *E. fishelsoni*. The life cycle begins with the formation of two small compartments within the mother cell and ends with the death of the mother cell and release of the offspring.

- *Epulopiscium fishelsoni*
- živi u simbiozi s ribom
Acanthus nigrofuscus





II. DIOBA BAKTERIJA

- većina bakterija i arheja dijele se **binarnom diobom**

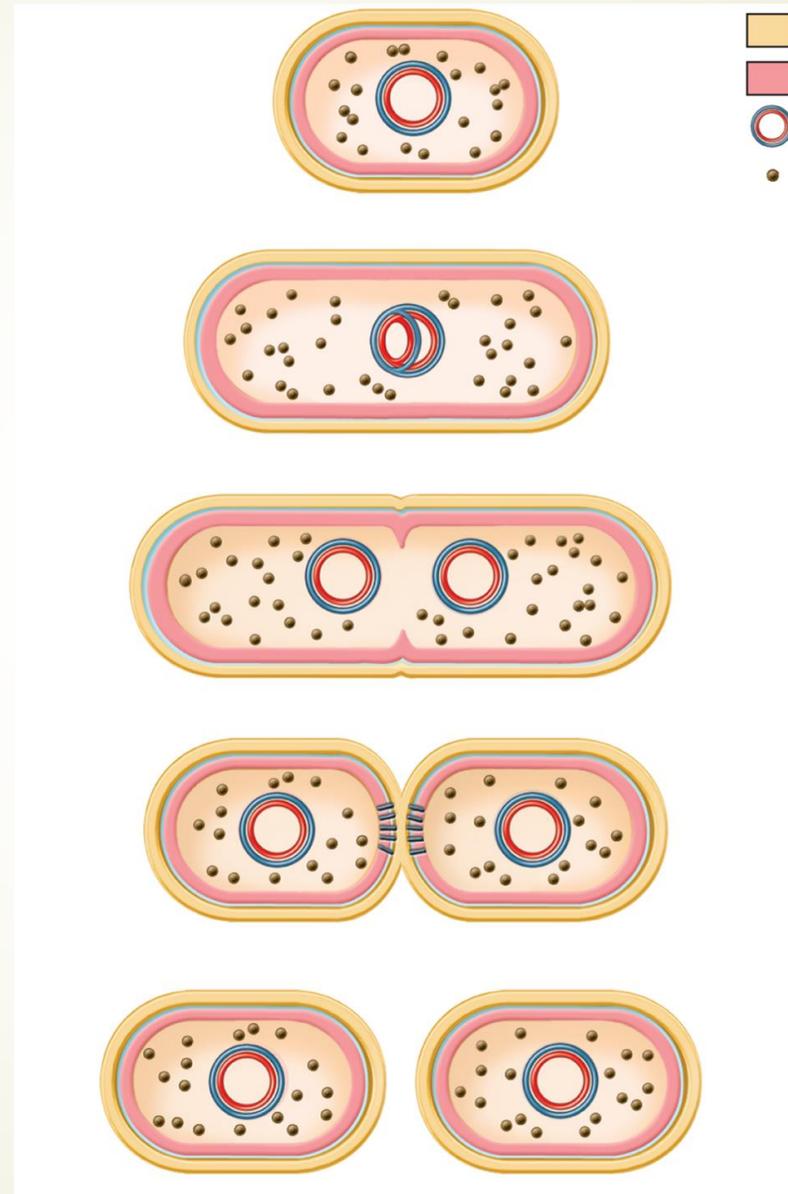
(a) A cell at early phase of cycle

(b) A cell prepares for division by enlarging its cell wall, plasma membrane, and overall volume. DNA replication starts.

(c) The septum grows inward as the chromosomes move toward opposite ends of the cell. Other cytoplasmic components are distributed to the two daughter cells.

(d) The septum is synthesized completely through the cell center, creating two separate cells.

(e) At this point, the daughter cells are divided. Some species separate completely as shown here, while others remain attached, forming chains, doublets, or other arrangements.

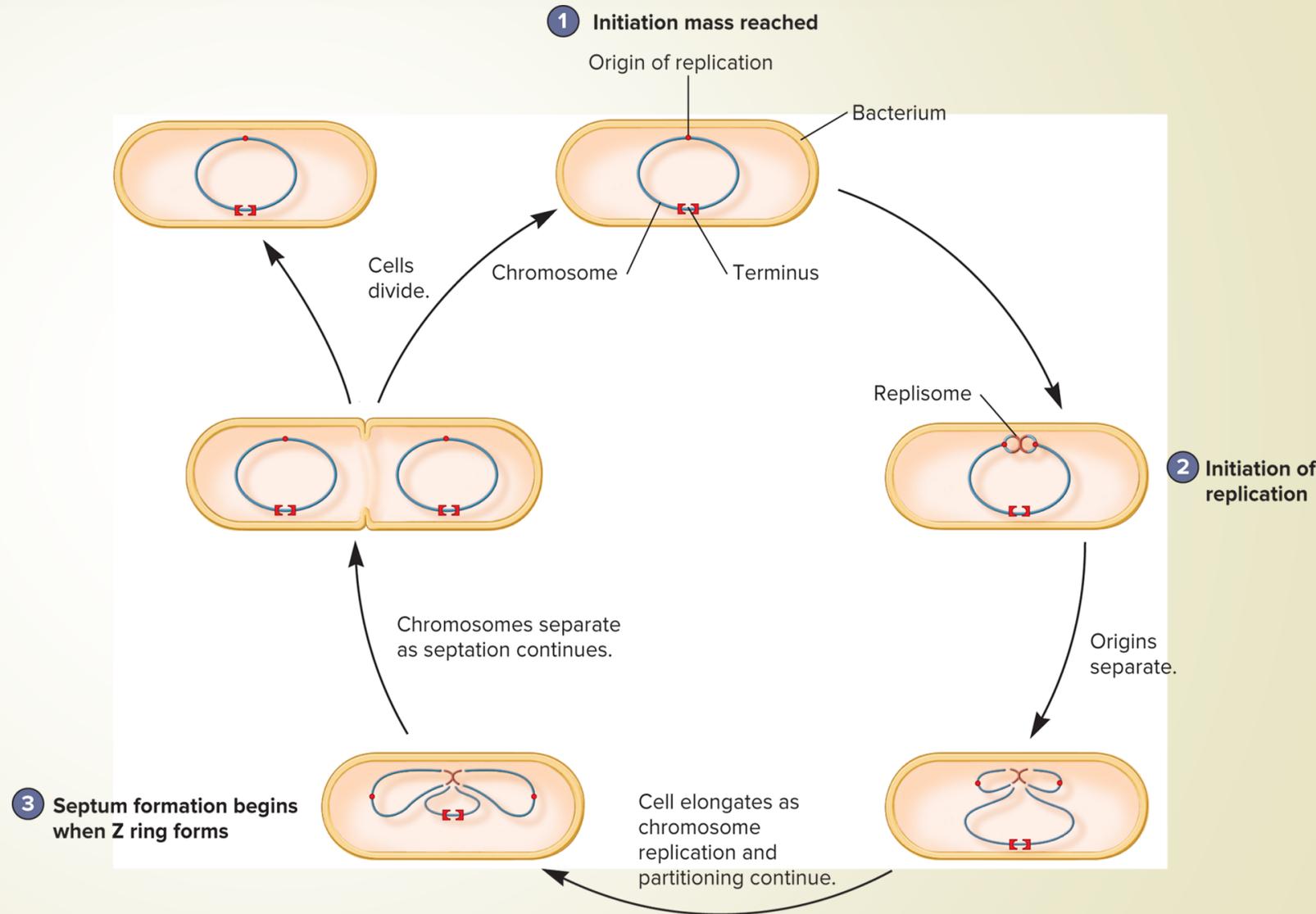


- Cell wall
- Cell membrane
- Chromosome
- Ribosomes

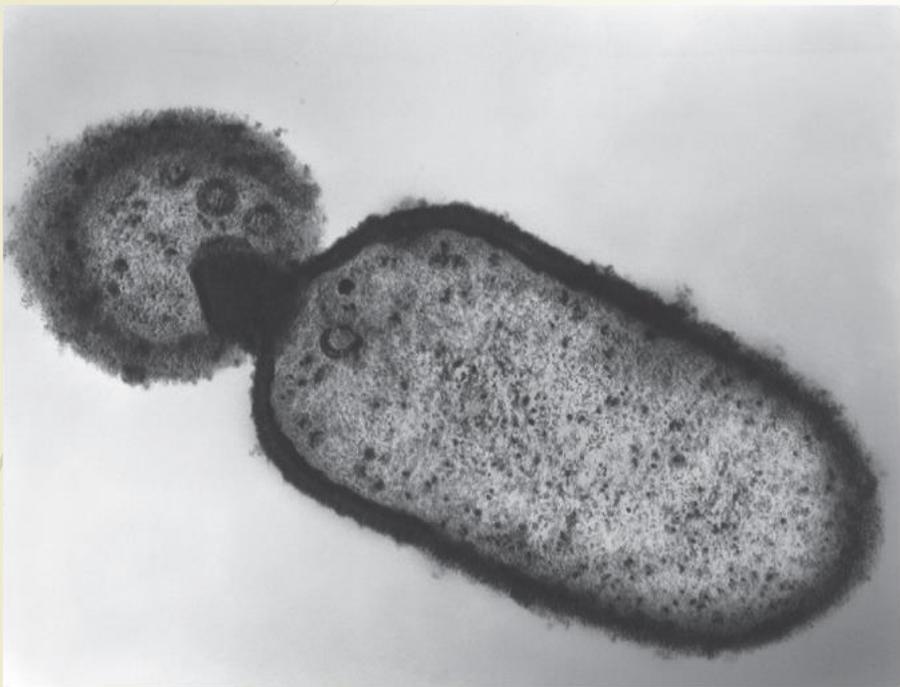
- **FtsZ protein** – homolog eukariotskog tubulina
Filamenting temperature-sensitive mutant Z
- sprječava stvaranje filamentozne tvorbe

BAKTERIJSKI CIKLUS BINARNE DIOBA PODIJELJEN JE U 3 FAZE

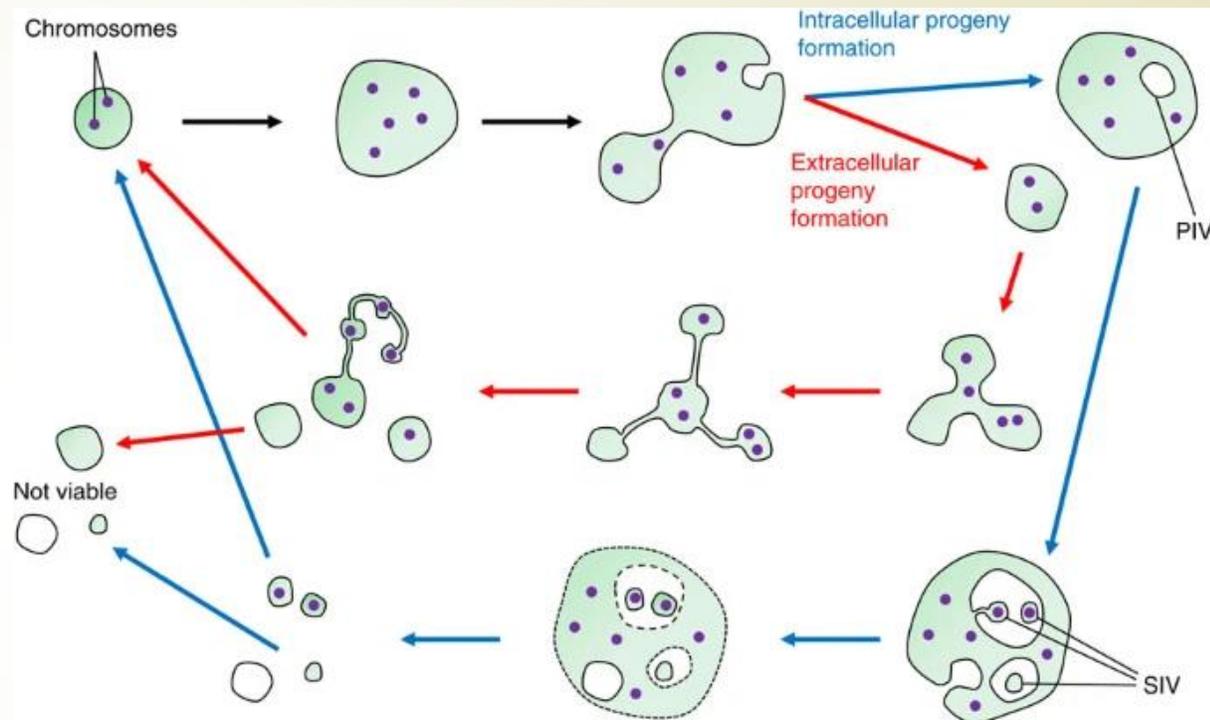
1. **Period rasta** – sličan G₁ fazi eukariotskog staničnog ciklusa
2. **Replikacija kromosoma** – odgovara S i M fazi eukariotskog ciklusa
3. **Citokineza** – stvaranje septuma i stanica kćeri



- ostale reproduktivne strategije:



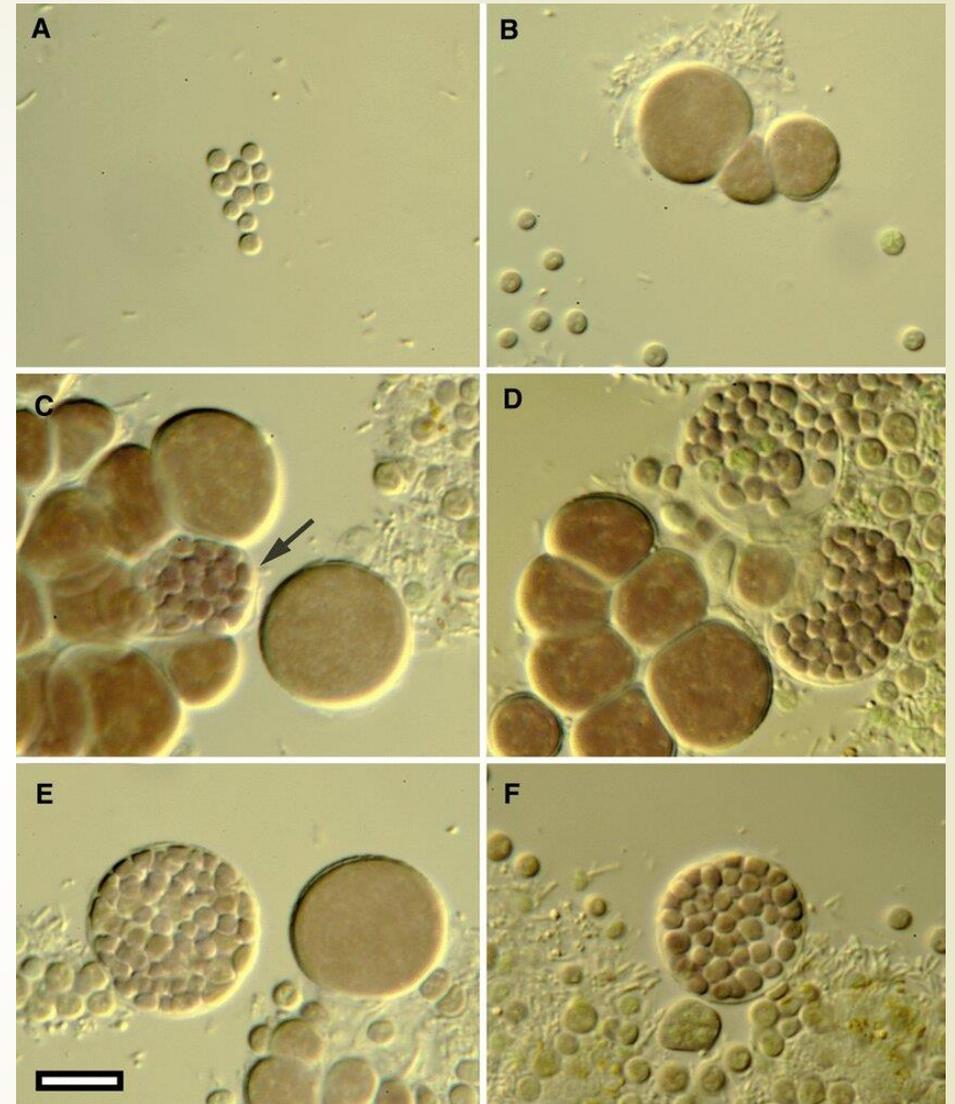
a) pupanje – *Listeria monocytogenes*



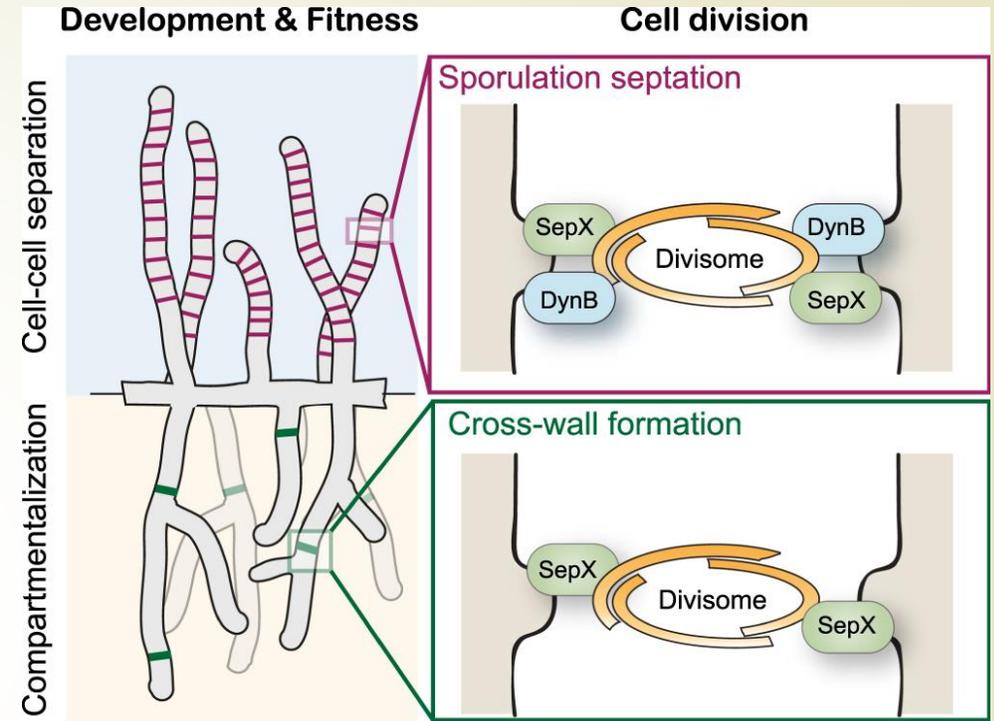
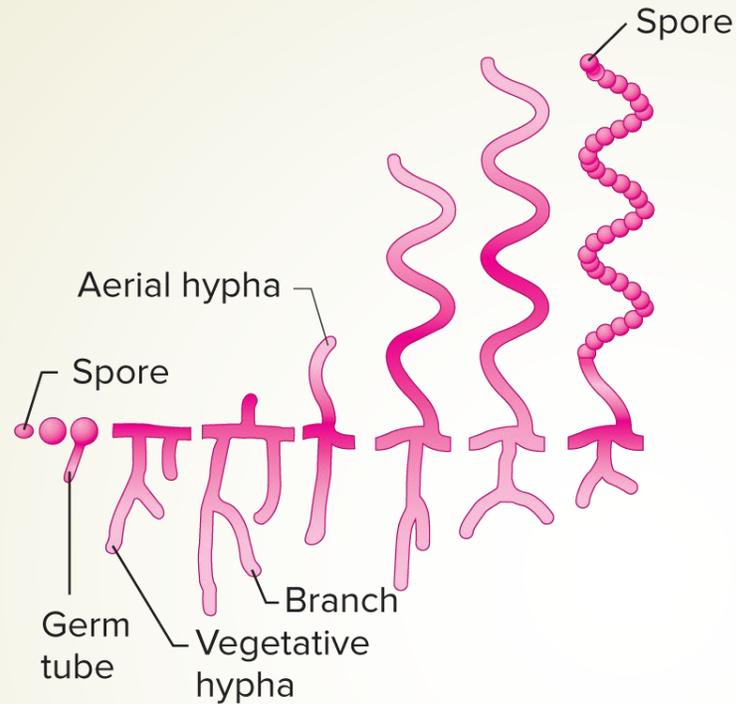
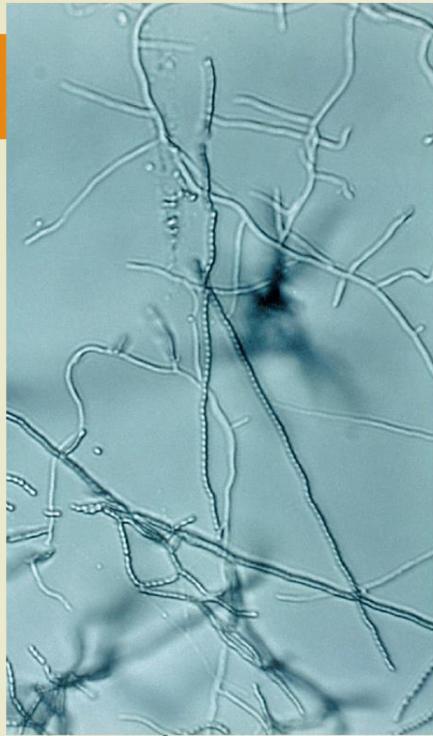
Studer, P., Staubli, T., Wieser, N. *et al.* Proliferation of *Listeria monocytogenes* L-form cells by formation of internal and external vesicles. *Nat Commun* 7, 13631 (2016). <https://doi.org/10.1038/ncomms13631>



b) višestruka dioba – cijanobakterije koljena Pleurocarpales (npr. *Democarpa* sp., *Waterburya* sp. *Pleurocapsa* sp....) – stvaranje **baeocita** – malih diferenciranih stanica koje se razlikuju od onih koje nastaju binarnom diobom



Bonthond, Guido & Shalygin, Sergei & Bayer, Till & Weinberger, Florian. (2021). Draft genome and description of *Waterburya* agarophytonicola gen. nov. sp. nov. (Pleurocapsales, Cyanobacteria): a seaweed symbiont. *Antonie van Leeuwenhoek*. 114. 10.1007/s10482-021-01672-x.

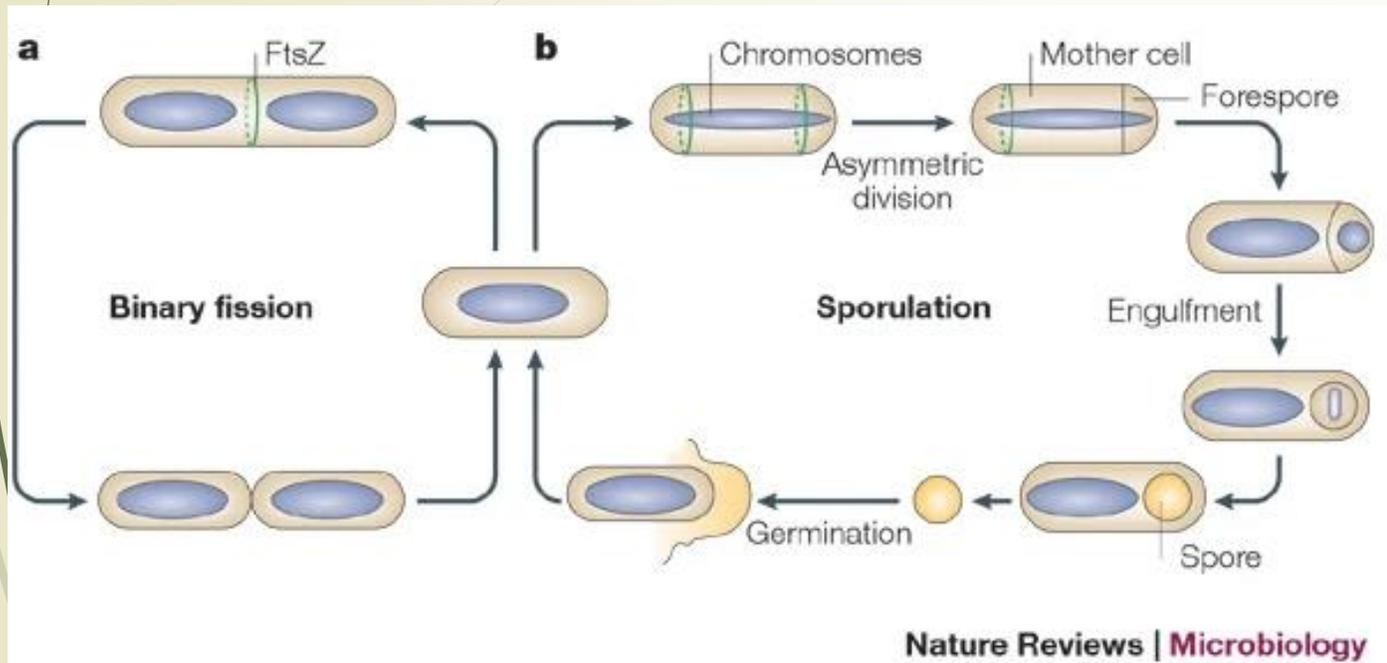


Bush, M.J., Gallagher, K.A., Chandra, G. *et al.* Hyphal compartmentalization and sporulation in *Streptomyces* require the conserved cell division protein SepX. *Nat Commun* 13, 71 (2022). <https://doi.org/10.1038/s41467-021-27638-1>

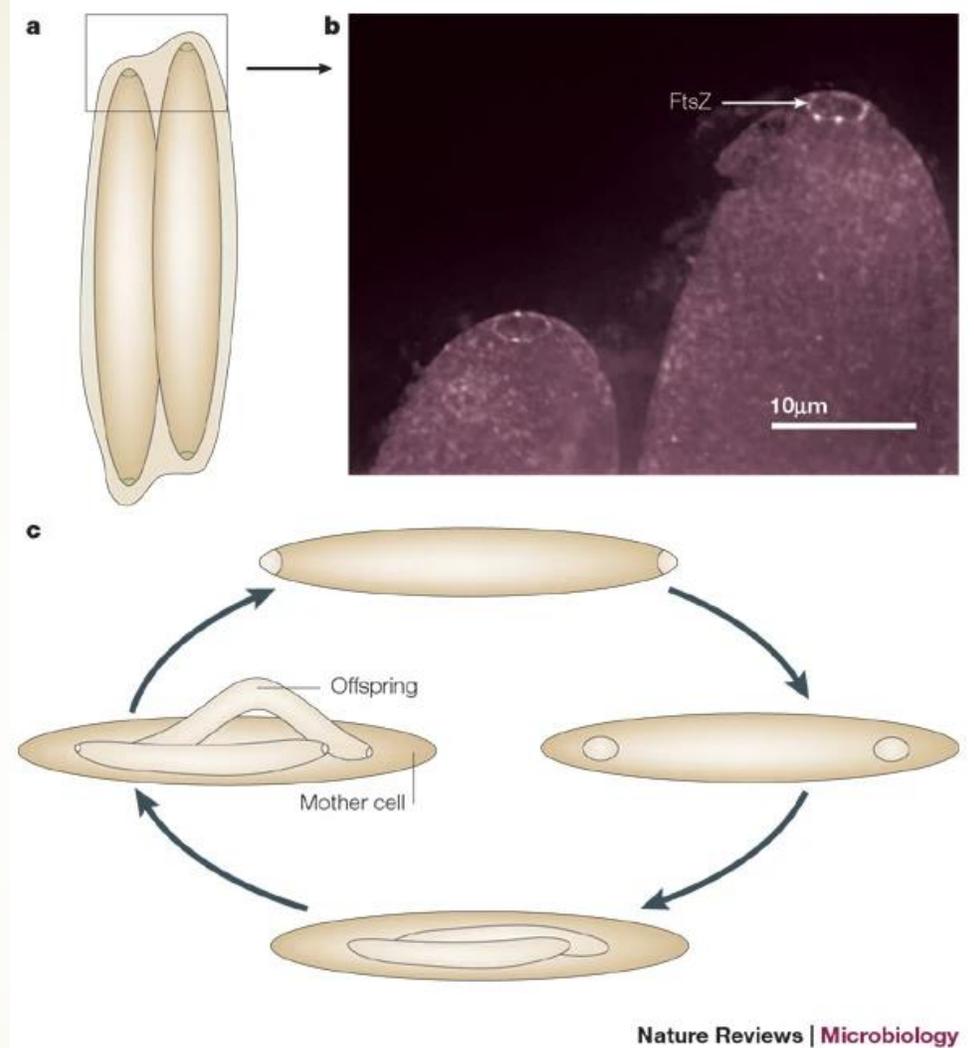
c) stvaranje spora

– streptomicete (*Streptomyces* spp.)

Filamentozne bakterije iz tla koje imaju **dva funkcionalna načina stanične diobe**: formiranje poprečnih pregrada u vegetativnim hifama (multinukleoidni odijeljci) i formiranje sporulacijskog septuma u zračnim hifama (formiranje unigenomskih spora).



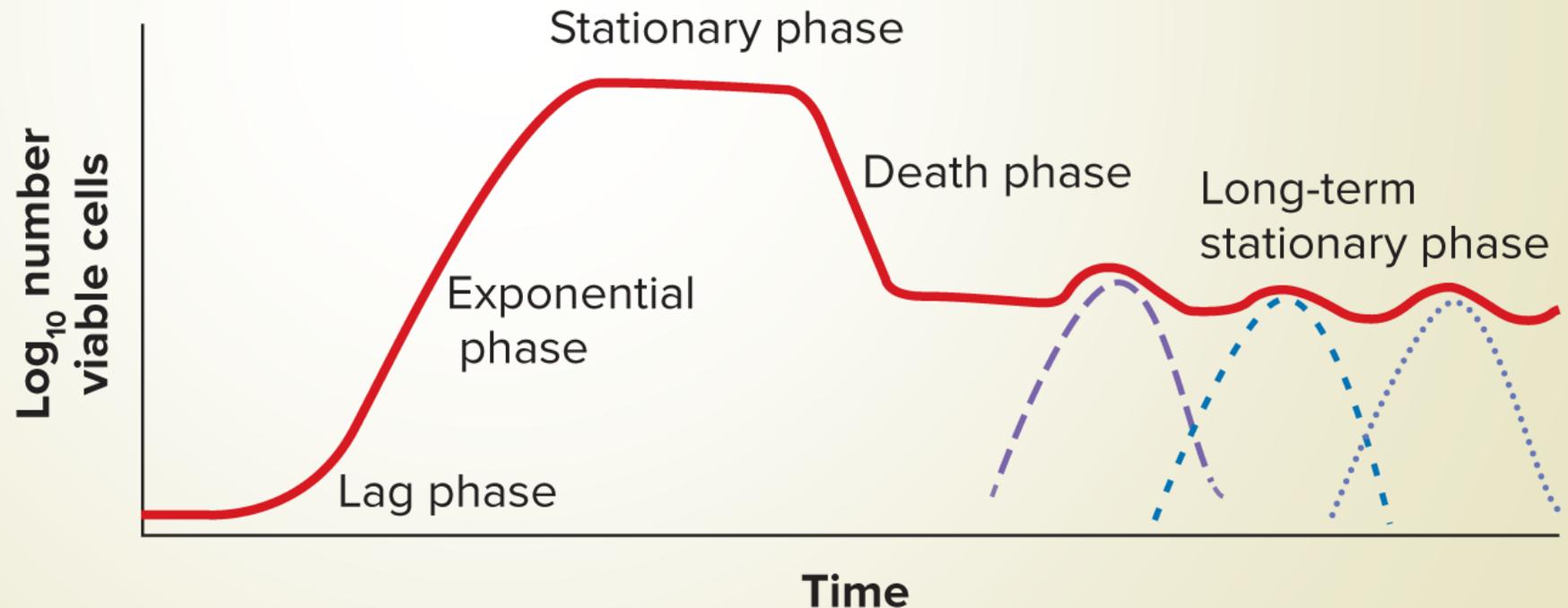
d) stvaranje endospora i promjena životnog ciklusa u nepovoljnim uvjetima (sporogene bakterije, npr. *Bacillus subtilis*)



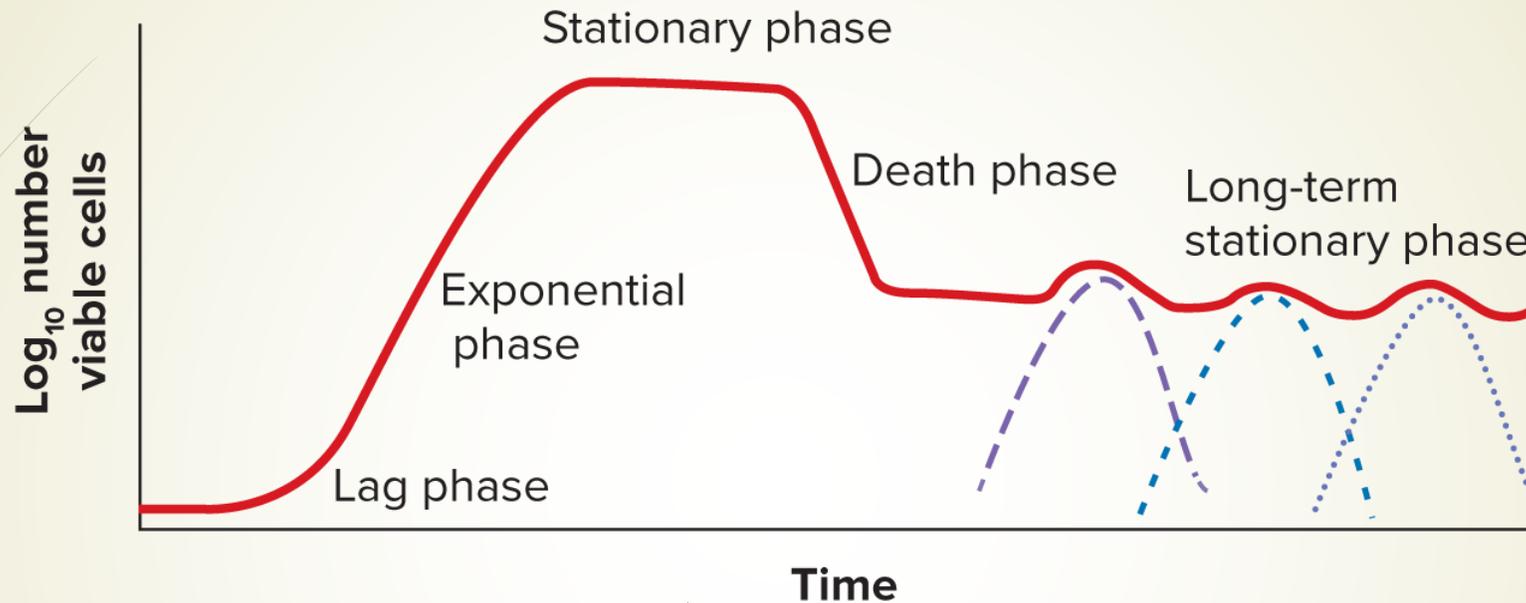
e) viviparnost – *Epulopiscium* sp.

BAKTERIJSKI RAST ODVIJA SE U PET FAZA

- „bakterijski rast” – povećanje broja bakterijskih stanica u populaciji
- moguće ga je pratiti i analizirati u tekućem hranjivom mediju
- krivulja rasta bakterija - specifičan oblik ovisan o bakterijskoj vrsti i upotrebnoj hranjivoj podlozi



BAKTERIJSKI RAST ODVIJA SE U PET FAZA



- **faza suzdržanog rasta – lag faza** (stvarno trajanje ovisi o statusu nacijepljenih stanica, prethodnim uvjetima uzgoja i broju stanica u inokulumu)
- **logaritamska ili eksponencijalna faza** (povećanje broja stanica geometrijskom progresijom; stanice se dijele makimalnom mogućom stopom rasta s obzirom na genetički potencijal, prirodu medija i uvjete okoliša)
- **stacionarna faza rasta** (10^9 stanica/ml; ravnoteža između stanične diobe i smrti; heterogena populacija) – produljena stacionarna faza (mjeseci ili godine)
- **logaritamska faza odumiranja**

- **generacijsko vrijeme** - vrijeme potrebno za udvostručenje broja mikroba u populaciji (konstantno za bakterijsku vrstu u standardnim uvjetima uzgoja)

Table 7.1 An Example of Exponential Growth¹

Time ² (min)	Generation Number	2^n	Number of cells ³ ($N_0 \times 2^n$)	$\log_{10} N_t$
0	0	$2^0 = 1$	1	0.000
20	1	$2^1 = 2$	2	0.301
40	2	$2^2 = 4$	4	0.602
60	3	$2^3 = 8$	8	0.903
80	4	$2^4 = 16$	16	1.204

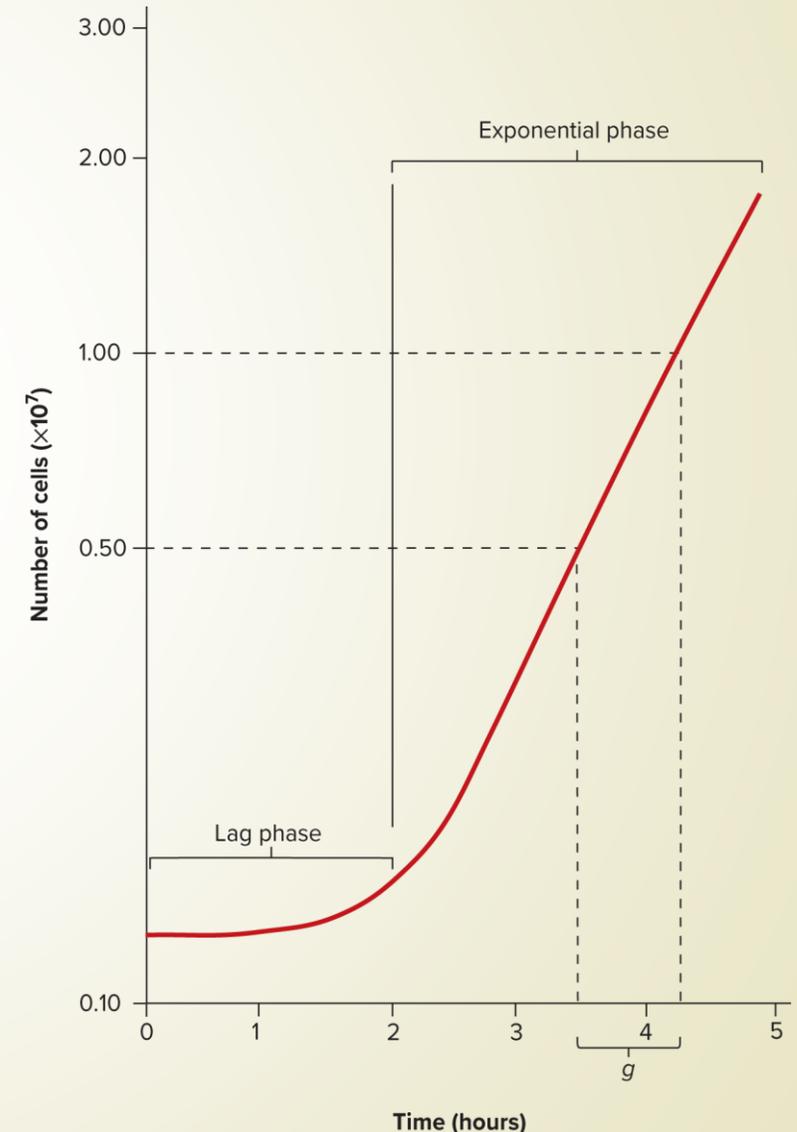


Table 7.2 Examples of Generation Times¹

Microorganism	Incubation Temperature (°C)	Generation Time (Hours)
Bacteria		
<i>Escherichia coli</i>	40	0.35
<i>Staphylococcus aureus</i>	37	0.47
<i>Mycobacterium tuberculosis</i>	37	~12
<i>Treponema pallidum</i>	37	33
Archaea		
<i>Pyrococcus abyssi</i>	90	0.67
<i>Sulfurisphaera tokodaii</i>	75	6
<i>Nitrososphaera viennensis</i>	37	45
Eukaryotes²		
<i>Euglena gracilis</i>	25	22
<i>Ceratium tripos</i>	20	48–72
<i>Saccharomyces cerevisiae</i>	30	2
<i>Monilinia fructicola</i>	25	30

30 min(37°C, pH 7.0, aeracija)

- generacijsko vrijeme u prirodnim uvjetima obično je puno dulje nego u laboratorijskim uvjetima; može varirati unutar bakterijske vrste ovisno o soju